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PSELAPHID BEETLES OF AN ILLINOIS PRAIRIE: THE POPULATION

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INTRODUCTION

In a previous report (Park, Auerbach & Wilson 1949) Peacock Prairie, near Evanston, Cook County, Illinois, was described and its diversified fauna of pselaphid beetles discussed from a qualitative viewpoint. This fauna was found to contain a species *(Reichenbachia subsimilis* Casey) that was known only from grassland, and its known distribution pattern appeared to support the Prairie Peninsula Hypothesis.

Since this report three additional species of pselaphids have been collected. Two of these were either directly associated with prairie ant societies or were generally reported in the literature as myrmecophilous. In addition, two of the three species lend additional support to the Prairie Peninsula Hypothesis.

The seasonal frequency of adult pselaphids in the upper three inches of prairie sod over a period of thirty-one months is discussed, chiefly with respect to population density per square meter. The prairie pselaphid fauna is separated into three seasonal population types. These data are reviewed with respect to two possible types of life cycle for these beetles.

ADDITIONAL FAUNAL AND ZOÖGEOGRAPHIC INFORMATION

Before discussing the seasonal aspects of the pselaphid populations at Peacock Prairie, it is desirable to evaluate new data. These latter were obtained primarily on three species that are associated more or less with prairie ants. All are new records for

Peacock Prairie and bring the faunal total to eight species.

The sixth species, *Rybaxis truncaticornis* Brendel, is not only new for the prairie but is a new record for the Chicago Area. The type locality for the species is Iowa, probably Iowa City (Brendel & Wickham 1890). In his excellent revision of the genus, Fall (1927) noted that all of the specimens seen by him were from Iowa and probably most, if not all, from Iowa City.

This species is represented in the collection of the senior author by specimens from Iowa City, Iowa, collected March 13, 1898, and from Urbana, Illinois, collected April 26, 1892. Some fifty years later *truncaticornis* was collected at Peacock Prairie under boards: a female taken March 4, 1949, and a male on April 9, 1949.

These collection dates are in general agreement although separated by some fifty years and represent specimens from three different localities. It is interesting to note that, although Peacock Prairie has been studied intensively for thirty-one months, the first *truncaticornis* record did not appear until the sixteenth month.

In the previous report on this prairie, it was felt that the prairie pselaphid fauna was fairly well known and that additional records might be of myrmecophilous species. This may be a partial answer to the absence of *truncaticornis* in earlier collections from Peacock Prairie. There is some confirmation for this suggestion in the literature. The only record known to the authors of a nearctic Rybaxis taken with ants, is that of Wickham (1900) who records *truncaticornis* from Iowa City on May 29th in leaves over the nest of *Lasius niger americanus* Emery. It may be that both the Iowa City and Peacock Prairie records were of the same nature, namely, *truncaticornis* may be a facultative synoeket. If this is so, this species may be able to exist in relatively un-

favorable situations through its ability to seek shelter in the dark, relatively humid nest of a dominant and ubiquitous host. Such an hypothesis would further suggest that forest species with facultative myrmecophilism, as well as symphiles, could exist in prairies and remain in the host nest during periods of relatively great aridity, e.g. from early summer into early autumn in this area. It has been suggested elsewhere (Park 1947) that facultative myrmecophilism may have enabled species of Batrisodes to spread northward from more southern to more northern forests. This same general tendency may apply also to the invasion of prairies from forests at the same latitude.

Finally, *Rybaxis truncaticornis* is known only from prairie in Iowa and Illinois so far, and becomes the second species of pselaphids to give support to the Prairie Peninsula Hypothesis (Fig. 1).
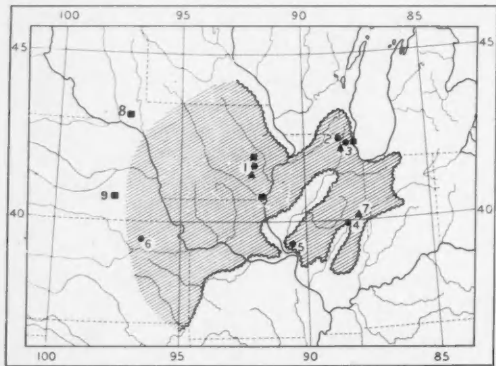

FIG. 1. Known distributions of three species of pselaphid beetles, *Reichenbachia subsimilis* Casey (black dots), *Reichenbachia peregrinator* Casey (black squares), and *Rybaxis truncaticornis* Brendel (black triangles), as examples of postglacial steppe relicts in the Prairie Peninsula. Localities are Iowa City, Iowa (1); Algonquin, Illinois (2); Peacock Prairie, Glenview, Illinois (3); Monticello, Illinois (4); Grafton, Illinois (5); Onaga, Kansas (6); Urbana, Illinois (7); southeastern South Dakota (8); eastern Nebraska (9). Roughly indicated outline of the Prairie Peninsula after Transeau, 1935. Scale: 1 inch equals 340 miles.

The seventh species, *Batrisodes globosus* (LeConte), is one of the most abundant and well known pselaphids in North America (Park 1947). It is known to inhabit the society of a variety of host ants. A female was taken on August 31, 1949, a male on October 7, 1949, and a female on October 20, 1949, in the nests of *Formica cinerea neocinerea* Wheeler. These were from three separate nests, and are the first records of *globosus* with *neocinerea*.

At Peacock Prairie the *neocinerea* mounds dot the prairie floor. They appear as tufted cushions, four to eight inches high and with a diameter of from one to three feet. Active nests have the top almost to quite bare of prairie vegetation. Fortunately this ant is well known. It is termed the "prairie ant," or the "prairie mound-building ant," and is reported to be the most conspicuous species of the prairies and wet meadows of Illinois (Gregg 1948).

In addition to providing a typical synoekete to the prairie fauna, the colonization of the area by *Formica neocinerea* also increases the number of niches that are available for the non-myrmecophilic prairie pselaphids. The relatively extensive nest galleries and chambers of this ant in the prairie humus can serve as avenues of relatively rapid penetration of the soil. This may be a more important aspect of prairie ecology than is realized generally. For example, on September 15, 1949, at about 5:30 P.M. a grass fire broke out on Peacock Prairie and destroyed the green plants. The prairie was revisited on September 27. On this date the surface soil layer was rather dry and charred, the vegetation was burned away except for the crumpled leaves of compass plants *(Silphium terebinthinaceum)* and the stems of rattlesnake master *(Eryngium yuccifolium)*. The ant nests stood out in sharp relief (Fig. 2). The contrast between the prairie floor after burning (Fig. 3) and with its full complement of vegetation (Park, Auerbach & Wilson 1949, Fig. 1) is very marked. Such epigean destruction suggested an examination of the scorched soil. A regularly collected sample of the sod of the top three inches, and one of the *neocinerea* nests were berlesed. Both of these samples contained large numbers of the typical soil fauna of microarthropods, e.g. Acarina, Collembola, Staphylinidae and Pselaphidae. The pselaphids belonged to the nonmyrmecophilic species *Bibloplectus integer*. There were seventy-six of these pselaphids in the nest sample. We shall return presently to this record in discussing the possible life cycle of prairie pselaphids. There is a possibility that these beetles were not actually in

FIG. 2. Nest of the prairie ant, *Formica cinerea neocinerea*, photographed 22 days after a grass fire at Peacock Prairie on September 15, 1949.

FIG. 3. Floor of Peacock Prairie, photographed 22 days after a grass fire on September 15, 1949. Note charred surface, crumpled leaves of the compass plants, and stalks of rattlesnake master.

the nest galleries, but were in the soil about the nest. This large number may have been coincidental, but several ant nests were similarly processed prior to this prairie fire and no individuals of this species of pselaphid were found.

It has been suggested by Sawyer (1946) that where prairie was protected from annual prairie fires in postglacial Illinois, small clumps of hazel marked the initial stage of penetration of forest into prairie. Since such fires are a natural hazard to grassland, the suggestion arises that prairie ant nests provide a shelter for microarthropods from burning vegetation.

In a broader sense, prairie ant nests may have a potential protective and recolonizing value for small prairie residents. It is noted by Gregg (1948) that the nests of *neocinerea* harbor both myrmecophilic and nonmyrmecophilic organisms. We may assume that where such organisms escape from the ants, they may survive (1) not only prairie fire, but (2) use the nest as a hibernaculum in winter, and (3) escape the relatively great aridity of late summer. Consequently the ant nests may be a partial ecological equivalent to the burrows of certain crayfish that were found to contain (Creaser 1931) numerous planktonic organisms after the temporary ponds had dried up in the summer.

The eighth species, *Reichenbachia peregrinator* Casey, was collected from beneath a board on January 17, 1950. It was described in 1897 from Iowa City and Keokuk, Iowa; Nebraska and South Dakota. Consequently the species is not only an addition to the Peacock Prairie fauna, it is a new record for the Chicago Area, and for Illinois. From its known distribution, *peregrinator* is seen to further support the Prairie Peninsula Hypothesis (Fig. 1).

At the time of writing, it can be concluded that the Pselaphidae offer good substantiating data for the existence of the Prairie Peninsula. Three out of eight species, or about 37 per cent, are known to have populations that extend more or less discontinuously from the Great Plains eastward into the Chicago Region. These three species are known from grassland but are unknown from forest communities.

KEY TO THE PSELAPHID BEETLES OF PEACOCK PRAIRIE

The pselaphids have been studied at Peacock Prairie for some two and half years, *e.g.*, from November, 1947, to May, 1950. It is believed that the pselaphid fauna is fairly well known in so far as taxonomic composition is concerned. The following key is to both sexes of the eight species known to occur in this prairie fragment. It is to be hoped that the key will serve to discriminate these species populations for the purposes of the present study.

Since other investigators that are working on grassland invertebrate populations in the United States may be expected to collect pselaphid beetles, it is hoped further that the key may be of assistance to them either in discrimination of these species, or in isolating other pselaphid species that will not key out in the following arrangement.

1   Antennae geniculate, with the first segment very long, at least half as long the funicle............................ 2
      Antennae not geniculate, and the first segment much shorter than described above................................... 3

2 (1) Last sternite nearly semicircular, nearly as long as wide, as long as the preceding two sternites united
             male *Rhexius insculptus* Leconte
      Last sternite very transverse, not as long as the preceding two sternites united
             female *Rhexius insculptus* LeConte

3 (1) Pronotum with a fine, longitudinal carina that bisects the basal third, from basal margin nearly to disc; minute beetles, distinctly less than one millimeter long.. 4
      Pronotum with base not longitudinally bisected by a carina; larger species, distinctly more than one millimeter long.. 5

4 (3) Seven sternites present, the seventh in the form of a narrow, longitudinally ovate penial plate (Fig. 8)
             male *Bibloplectus integer* (LeConte)
      Six sternites present (Fig. 8)
             female *Bibloplectus integer* (LeConte)

5 (3) Distal segment of maxillary palpi very long and conspicuous, with a slender, pedunculate base and the distal two-thirds swollen and lengthily setose........ 6
      Distal segment of maxillary palpi not as described.... 7

6 (5) Metasternum medially longitudinally sulcoid; last sternite large, semicircular, nearly as long as first visible sternite
             male *Pselaphus fustifer* Casey
      Metasternum medially tumid; last sternite transversely semilunate, about a third as long as first visible sternite
             female *Pselaphus fustifer* Casey

7 (5) General body pubescence in the form of thin, flattened, elongate scales, especially obvious on posterior margins of sternites and posterior elytral margins; last three segments of maxillary palpi each with a conspicuous setoid appendage............................ 8
      General body pubescence in the form of short, normally aciculate setae........................ 9

8 (7) Abdomen with the ventral outline concave from a lateral view, the sternites medially flattened
         male *Pilopius lacustris* Casey

Abdomen with the ventral outline convex from a lateral view, the sternites tumid
         female *Pilopius lacustris* Casey

9 (7) Lateral abdominal margins well formed on first two segments.. 10

Lateral abdominal margins absent and replaced by carinae 15

10 (9) Pronotum with free antebasal foveae; elytra with no subhumeral fovea on flank.... 11

Pronotum with antebasal foveae connected by a deep arcuate sulcus; elytral flank with a subhumeral fovea 14

11 (10) Basal abdominal carinae approximate and divergent, separated at base by a transverse distance that never notably exceeds the maximum mutual separation of the sutural striae of elytra.... 12

Basal abdominal carinae less approximate, always separated at base by more than the interspace of the elytral sutural striae, but never separated by more than one-fourth of the total width of the first visible tergite 13

12 (11) Abdomen with ventral outline concave; basal abdominal carinae of first visible tergite separated at base by the full interspace of the sutural elytral striae
         male *Reichenbachia subsimilis* Casey

Abdomen with ventral outline straight to convex; basal abdominal carinae separated at base by less that the interspace of the sutural elytral striae
         male *Reichenbachia peregrinator* Casey

13 (11) Abdomen with ventral outline concave; last visible sternite large, medially flattened toward base
         male *Reichenbachia peregrinator* Casey

Abdomen with ventral outline convex; last visible sternite not as described
         female *Reichenbachia peregrinator* Casey

14 (10) Distal antennal segment bearing an oblique tooth near base; second ventral segment bearing a subquadrate process from posterior margin
         male *Rybaxis truncaticornis* Brendel

Distal antennal segment not toothed; second ventral segment without such a process
         female *Rybaxis truncaticornis* Brendel

15 (9) Tenth antennal segment bearing a small fovea at base of ventral face
         male *Batrisodes globosus* (LeConte)

Tenth antennal segment not bearing a fovea
         female *Batrisodes globosus* (LeConte)

SEASONAL POPULATION OF ADULTS IN THE UPPER SOD LAYER

Since the only previous work on population densities of Pselaphidae was of a theoretical nature, involving species of tropical American forests (Park 1942), an effort was made to estimate the size and seasonal fluctuations of the limited pselaphid fauna of Peacock Prairie.

Two methods were used to obtain these beetles. Regular examination of the prairie was started on November 12, 1947. At first this consisted of taking a 0.08 square meter sample of prairie sod and associated soil to a depth of three inches. One such sample was collected on each trip and the sample was taken at random. Each sample averaged 5000 grams dry weight. It was placed in a Berlese funnel and the pselaphids that were obtained were identified, sexed, counted and examined for ectoparasitic mites.

TABLE 1. Pselaphid Collections at Peacock Prairie.

Date	Biblo-plectus		Rhexius		Reichenbachia subsim.		Rybaxis		Psela-phus		Pilopius		Trip total
	Sod	Brd	Sod	Brd	Sod	Brd	Sod	Brd	Sod	Brd	Sod	Brd	
1947													
xi. 12....	26	0	0	0	0	0	0	0	0	0	0	0	26
xi. 19....	3	0	0	0	0	0	0	0	0	0	0	0	3
xi. 26....	1	0	0	0	1	0	0	0	0	0	0	0	2
xii. 3....	0	0	0	0	0	0	0	0	0	0	0	0	0
xii. 10....	7	0	0	0	0	0	0	0	0	0	0	0	7
xii. 17....	0	0	0	0	0	0	0	0	0	0	0	0	0
xii. 23....	0	0	0	0	0	0	0	0	0	0	0	0	0
1948													
i. 6....	0	0	0	0	0	0	0	0	0	0	0	0	0
i. 13....	2	0	0	0	0	0	0	0	0	0	0	0	2
iii. 22....	0	0	0	0	0	0	0	0	0	0	0	0	0
iv. 1....	1	0	0	0	0	0	0	0	0	0	0	0	1
iv. 8....	4	0	0	0	2	1	0	0	0	1	0	1	9
iv. 11....	0	0	0	0	0	5	0	0	0	0	0	1	6
iv. 15....	0	0	0	0	0	2	0	0	0	0	0	1	3
iv. 22....	7	0	0	0	0	3	0	0	0	0	0	2	12
iv. 27....	7	0	1	0	0	1	0	0	0	0	0	2	11
v. 7....	3	0	1	0	1	0	0	0	0	0	0	0	5
v. 15....	1	0	2	0	4	2	0	0	0	0	0	0	9
v. 23....	2	0	0	0	0	0	0	0	0	0	1	1	4
vi. 3....	3	0	0	0	1	0	0	0	0	0	0	0	4
vi. 13....	0	0	0	0	0	0	0	0	0	0	0	0	0
vi. 21....	0	0	0	0	0	0	0	0	0	0	0	0	0
vi. 23....	1	0	0	0	0	0	0	0	0	0	0	0	1
vi. 29....	0	0	0	0	1	0	0	0	0	0	0	1	2
vii. 1....	8	0	0	0	0	0	0	0	0	0	0	0	8
vii. 7....	3	0	1	0	1	0	0	0	0	0	1	0	6
vii. 15....	0	0	0	0	0	0	0	1	0	0	0	0	1
vii. 23....	12	0	1	0	0	0	0	0	0	0	0	0	13
vii. 27....		0		0		0		0		0		0	0[2]
viii. 4....	5	0	0	0	4	1	0	0	0	0	0	0	10
viii. 11....	3	0	0	0	1	0	0	0	0	0	0	0	4
viii. 19....	0	0	0	0	1	0	0	0	1	0	0	0	2
viii. 25....	0	0	0	0	1	0	0	0	0	0	0	0	1
ix. 1....	0	0	0	0	0	0	0	0	0	0	0	0	0
ix. 9....	0	0	0	0	0	0	0	0	0	0	0	0	0
ix. 15....	0	0	0	0	2	0	0	0	0	0	0	0	2
ix. 22....	2	0	0	0	0	0	0	0	0	0	0	0	2
ix. 29....	11	0	0	0	0	0	0	0	0	0	0	0	11
x. 7....	0	0	1	0	1	0	0	0	0	0	0	0	2
x. 13....	7	0	0	0	0	0	0	0	1	0	0	0	8
x. 20....	1	0	0	0	0	0	0	0	0	0	0	0	1
x. 27....	2	0	0	0	0	0	0	0	0	0	0	0	2
xi. 3....	3	0	0	0	0	0	0	0	0	0	0	0	3
xi. 10....	1	0	1	0	0	0	0	0	0	0	0	0	2
xi. 17....	1	0	0	0	0	0	0	0	1	0	0	0	2
xi. 24....	9	0	0	0	0	0	0	0	1	0	0	0	10
xii. 3....	1	0	0	0	1	0	0	0	0	0	0	0	2
xii. 8....	1	0	0	0	0	0	0	1	0	0	0	0	2
1949													
iii. 4....	1	0	0	0	0	2	0	1	0	0	0	3	7
iii. 26....	2	0	0	0	2	0	0	0	0	0	0	0	4
iv. 1....	0	0	0	0	1	0	0	0	0	0	0	0	1
iv. 9....	7	0	0	0	2	0	1	0	0	0	0	0	10
iv. 16....	1	0	0	0	0	0	0	0	0	0	1	0	2
iv. 22....	1	0	0	0	4	2	0	0	0	0	0	2	9
v. 1....	10	0	2	0	0	0	0	0	0	0	0	0	12
v. 6....	1	0	0	0	0	0	0	0	0	0	0	0	1
v. 16....	27	0	5	0	0	0	0	0	0	0	0	0	32
v. 30....	0	0	0	0	0	0	0	0	0	0	0	0	0
vi. 12....	0	0	0	0	1	0	0	0	0	0	0	0	1
vi. 15....	4	0	0	0	0	1	0	0	0	0	0	0	5
vi. 21....	1	0	0	0	2	0	0	0	0	0	0	0	3
vii. 8....	4	0	0	0	0	0	0	0	0	0	0	0	4
vii. 28....	0	0	0	0	0	0	0	0	0	0	0	0	0
viii. 11....	0	0	0	0	1	0	0	0	0	0	0	0	1
viii. 31....	0	0	0	0	0	0	0	0	0	0	0	0	0

Date	Biblo-plectus		Rhexius		Reichen-bachia subsim.		Rybaxis		Psela-phus		Pilopius		Trip total
	Sod	Brd	Sod	Brd	Sod	Brd	Sod	Brd	Sod	Brd	Sod	Brd	
ix. 14....	0	0	0	0	0	0	0	0	0	0	0	0	0
ix. 27....	9	0	1	0	1	0	0	0	0	0	0	0	11
x. 7....	0	0	0	0	0	2	0	0	0	0	0	4	6
x. 20....	1	0	0	0	0	4	0	0	0	0	0	5	10
xi. 1....	0	0	0	0	0	2	0	0	0	1	0	2	5
xi. 8....	5	0	0	0	0	0	0	0	0	0	0	2	7
xi. 17....	5	0	0	0	0	5	0	0	0	1	0	8	19
xi. 25....	2	0	0	0	1	0	0	0	0	0	0	0	3
xi. 29....	11	0	0	0	0	14	0	0	0	2	0	26	53
xii. 6....	17	0	0	0	0	0	0	0	0	0	0	1	18
xii. 13....	1	0	0	0	0	0	0	0	0	0	0	0	1
1950													
i. 10....	1	0	0	0	0	0	0	0	0	1	0	4	6
i. 17....	1	0	0	0	0	0	0	0	2	1	0	8	12
i. 24....	0	0	0	0	2	3	0	1	0	3	0	37	46
ii. 23....	1	0	0	0	0	0	0	0	0	0	0	0	1
iii. 24....	0	0	0	0	0	0	0	0	0	0	0	0	0
iv. 1....	5	0	0	0	1	2	0	0	0	1	0	7	16
iv. 14....	0	0	0	0	1	1	0	0	1	1	0	1	5
v. 11....	2	0	1	0	0	0	0	0	0	0	0	4	7
v. 25....	3	0	0	0	0	0	0	0	0	0	0	0	3
Totals...	261	0	17	0	36	58	0	3	9	12	3	123	522

2 No sod samples collected on July 27, 1948.

Later, on April 1, 1948, these sod samples were augmented by regular examination of boards placed at random over the prairie, following the general technique of Cole (1946). Twelve boards, with an average area of 0.25 square meters each, were examined on each trip. The lower surfaces were relatively moist, cool, and dark and served to "trap" some pselaphid beetles.

These collections at Peacock Prairie are given in Table 1. In this table "sod" refers to individuals extracted from the top three inches of prairie sod and its associated soil by means of a modified Berlese funnel; "brd" refers to those individuals collected with an aspirator apparatus from the lower surface of boards laid at random on the prairie floor.

In Table 1 the adults of six of the species collected at Peacock Prairie are listed for the 85 trips taken between November, 1947, and May, 1950. The uncommon *Rybaxis truncaticornis*, taken three times beneath boards, may be a facultative synoekete of the prairie ant, *Formica cinerea neocinerea*. The locally rare *Reichenbachia peregrinator* is known from a single board record and is not included, nor is *Batrisodes globosus*, known at the prairie only from ant nests. These ant-nest inhabitants represent a special aspect of the prairie ecology and are dealt with later.

In all, 522 specimens were collected from the two habitats, sod and beneath boards, on the prairie floor. Of these, 326 or about 60% were berlesed from the sod; 196 or about 40% were collected from beneath boards. The distribution of the six species as between these two habitat niches reflects the species differences within the pselaphid population as a whole.

Collecting beneath boards was not begun until

April, 1948, so that the number of individuals taken in this habitat niche may be potentially slightly higher than the data show.

These six species are analyzed in Table 2 from the viewpoint of habitat niche distribution, and species frequency within the period of this investigation.

TABLE 2. Species and Habitat Niche Frequencies.

Species	HABITAT NICHE				Spe-cies Total	Per cent
	Sod Num-ber	Per cent	Board Num-ber	Per cent		
Bibloplectus integer.......	261	50.0	0	0.0	261	50.0
Rhexius insculptus....	17	3.2	0	0.0	17	3.2
Reichenbachia subsimilis.....	36	6.8	58	11.1	94	17.9
Rybaxis truncaticornis.	0	0.0	3	0.6	3	0.6
Pselaphus fustifer........	9	1.0	12	2.5	21	3.5
Pilopius lacustris......	3	0.6	123	23.5	126	24.1
Totals.....	326	61.6	196	37.7	522	99.3

From Table 2 it is seen that the minute euplectine, *Bibloplectus integer* makes up more than half of the total floor population; the largest in size, *Pilopius lacustris*, accounts for about a fourth of the total; three species (*Bibloplectus integer*, *Reichenbachia subsimilis*, and *Pilopius lacustris*) form 92%, and the other species only 8% of all floor individuals collected.

These six species show a differential habitat niche distribution. Two species (*Bibloplectus integer* and *Rhexius insculptus*) were taken only in berlesed sod samples; *Rybaxis truncaticornis* was collected only beneath boards; of the other three species, *Pilopius lacustris* was rare in sod and abundant under boards, *Reichenbachia subsimilis* and *Pselaphus fustifer* were more or less evenly divided between the two habitats.

Bringing these data up to date, it will be recalled that one individual of the locally rare *Reichenbachia peregrinator* was collected beneath a board on January 17, 1950. Added to this are the beetles taken in ant nests. These included three specimens of *Batrisodes globosus*, frequently reported from ant nests (Park 1947), and the two sod species that were taken from ant nests following prairie fires, e.g., 79 *Bibloplectus integer* and one *Rhexius insculptus*. This gives a total of 606 pselaphids collected in the thirty-one month period, or about nineteen per month average. This does not include the critical check of the data reported later in this paper.

Since the number of trips to the prairie varied from one to six per month, the collections are examined in Table 3 in terms of corrected monthly averages.

TABLE 3. Monthly Frequency of Pselaphidae at Peacock Prairie.

Month	Biblopectus	Rhexius	Reichenbachia	Rybaxis	Pselaphus	Pilopius	Total psl./ month	Total No. of trips	Average psel./ trip
1947									
November....	30	0	1	0	0	0	31	3	10
December.....	7	0	0	0	0	0	7	4	2
1948									
January......	2	0	0	0	0	0	2	2	1
February.....	0	0	0	0	0	0	0	0	0
March........	0	0	0	0	0	0	0	1	0
April.........	19	1	14	0	1	7	42	6	7
May.........	6	3	7	0	0	2	18	3	6
June.........	4	0	2	0	0	1	7	5	1
July.........	23	2	1	0	1	1	28	5	6
August.......	8	0	8	0	1	0	17	4	4
September....	13	0	2	0	0	0	15	5	3
October......	10	1	1	0	1	0	13	4	3
November....	14	1	0	0	2	0	17	4	4
December.....	2	0	1	0	1	0	4	2	2
1949									
January......									
February.....									
March........	3	0	4	1	0	3	11	2	5
April.........	9	0	9	1	0	3	22	4	5
May.........	38	7	0	0	0	0	45	4	11
June.........	5	0	4	0	0	0	9	3	3
July	4	0	0	0	0	0	4	2	2
August.......	0	0	1	0	0	0	1	2	0.5
September....	9	1	1	0	0	0	11	2	5
October......	1	0	6	0	0	9	16	2	8
November....	23	0	22	0	4	38	87	5	17
December.....	18	0	0	0	0	1	19	2	9
1950									
January......	2	0	5	1	7	49	64	3	21
February.....	1	0	0	0	0	0	1	1	1
March........	0	0	0	0	0	0	0	1	0
April.........	5	0	5	0	3	8	21	2	10
May.........	5	1	0	0	0	4	10	2	5
Totals.....	261	17	94	3	21	126	522	85	5.9

Table 3 is a reorganization of the data of Table 1 on a monthly basis. From this it will be seen that the average number of pselaphids per trip is between five and six. This average includes both sod analyses and collections beneath boards, but not the pselaphids taken in ant nests. Since this monthly average is composite, it was felt that a special examination of the sod samples alone might give a more accurate picture through the 2.5 year period, especially since each sod sample covered an equivalent area and volume of sod, more or less, and there was less chance of overlooking minute species.

This has been attempted for the abundant *Bibloplectus integer* (Fig. 8). This species makes up about 50% of the fauna at Peacock Prairie and its seasonal distribution is given in the accompanying illustration (Fig. 4). In the figure, the average monthly population per 0.08 square meter of prairie sod is graphed for the first twenty-four-month period. In so far as the data go, it is felt that they are reliable.

Each sod sample was kept in a Berlese funnel until the soil was very dry, e.g. for a week or longer. Then the beaker of alcohol at the spout of the funnel was removed and the contents examined, bit by bit, with a high-power dissecting binocular. Even so, some individuals may have been killed by the heat in the funnel before they fell into the beaker, and furthermore, some pselaphids may have been missed in making the quantitative counts of the beaker residue. With this in mind, it should be noted that these possible sources of error in the method would be spread over the whole period of the study, so that the monthly averages should be relatively accurate. It is obvious that such errors would be on the parsimonious side with respect to abundance of individuals.

The population graph is incomplete for February, 1948, and for January and February, 1949, and it is assumed that during these three months the upper three inches of sod held no pselaphids. Indirect support for this assumption will be noted later. Initially, the method of taking sod samples consisted in placing a stout wire frame on the ground, cutting the sod around the frame, and collecting the enclosed sample to a depth of three inches. This method tended to give a series of sod samples of uniform area and relatively uniform volume. When winter thaws were followed by low temperatures, the sod was frozen so solidly that an accurate sample could not be obtained by digging through ice. Other methods are under consideration for the continuation of this study beyond the two year period.

Several suggestive features emerge from examination of Figure 4. There appear to be two periods of adult abundance in the three inch layer of sod at Peacock Prairie. One period is the early autumn— early winter, with a peak of abundance coming in September (1949) and November (1947, 1948); the second period is the late spring-summer, with a peak of abundance coming in May (1949) and April and July (1948). With the exception of the July, 1948 peak, the years 1948 and 1949 are in general agreement with respect to the relative rise and fall of numbers of adult Biblopectus at the soil layer examined. The two years differ in the numbers of adults collected. This suggests that those factors that govern the frequency of populational events are not necessarily the same, in kind or degree, as those factors that govern the amplitude of populational events.

The diatom population near the surface of the North Atlantic and in such large lakes as Lake Michigan and Lake Erie also undergoes an autumnal pulse and a vernal pulse. In this instance, it seems fairly well established that the pulses result from rapid algal reproduction as a consequence of a combination of factors that include light intensity, water temperature, and the concentration of dissolved nitrates and phosphates. With respect to Biblopectus the situation is much more obscure. The population pulses in autumn and spring may be purely coincidental with those of aquatic plankton, or they may be the consequence of a combination of factors that
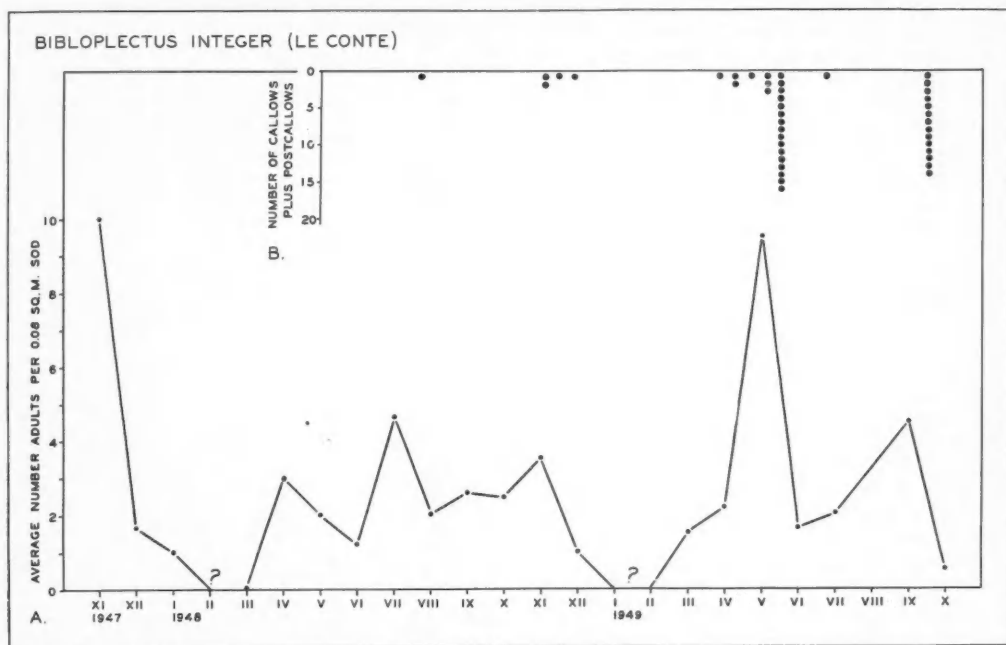
FIG. 4. *Bibloplectus integer* (LeConte). A. Average number of adults per 0.08 square meter of prairie sod, per month, for two years. B. Seasonal distribution of freshly emerged adults (callows and postcallows).

include soil temperature and soil moisture operating in conjunction with the rhythmic cycle of pupation. These aspects will be discussed further in the next section.

There is also the possibility that the spectacular increases in Bibloplectus adults are the consequence of sampling aggregations of these beetles. This is statistically unlikely in view of random sampling over the prairie in conjunction with the seasonal repetition of peaks of abundance.

CRITICAL CHECK OF BIBLOPLECTUS POPULATION DENSITY

After this two year study of seasonal collections had been analyzed, it was deemed advisable to set up some kind of check of the data. One that came to mind was the collecting of one square meter of sod to see if the number of contained Bibloplectus corresponded to the number that would have been collected from a series of discontinuous samples of smaller size.

One square meter of prairie sod was selected. This was located in an area where small samples had been collected for several years. The square meter was surrounded by previous digging scars and held the typical prairie vegetation. This square meter was collected to a depth of three inches on June 20, 1950, and brought to the laboratory.

Our facilities for berlesing samples allowed only a

half meter of sod to be extracted at a time. The other half was stored in a refrigerator until July 4, 1950, when the last half was berlesed. Not only were the berlesates saved and examined a second time to be sure that no beetles had been overlooked, but random samples of sod and soil in the funnels were pulled apart and examined to be sure that these small beetles were being driven from the funnels.

The results of this test are given in Table 4.

TABLE 4. Number of Bibloplectus in One Square Meter.

FIRST FRACTION		SECOND FRACTION	
Date of Berlesate	Yield	Date of Berlesate	Yield
June 21, 1950	3	July 5, 1950	7
June 22	3	July 6	0
June 23	1	July 7	1
June 24	4	July 11	1
June 25	4	July 25	0
June 27	3		
June 28	1		
June 29	0		
June 30	0		
July 3	2		
July 4	1		
Total	22	Total	9

Total for square meter: 31

Lack of facilities prevented the berlesing of the entire square meter simultaneously. In the field the square meter was deposited in several paper-lined gunny sacks, and the square meter was thoroughly mixed up so that the berlesates of the first fraction (Table 4) contained half of a square meter in volume but taken from various places within the square meter frame. This was a most fortunate circumstance since it will be seen from Table 4 that the first fraction of fresh sod yielded 22 specimens whereas the second fraction, stored for some fifteen days in a refrigerator, yielded only 9 beetles, or about 40 per cent of the first fraction. This suggests that accurate results can not be anticipated unless fresh sod is used in quantitative work.

For this reason, only the first half meter of fresh sod may be used in checking the small sample data. From Table 1 we see that in June, 1948, five trips were made, five small samples berlesed, and these yielded four *Biblopectus integer;* in June, 1949, three trips were made, three small samples were berlesed, and yielded five of this species.

Since there are about six of the small, or 0.08 square meter samples, in a half square meter, a half square meter should have yielded about 24 beetles in June, 1948, and about 30 beetles in June, 1949. This assumes that the small samples were alike, and that the local weather and ecological conditions were similar throughout the given month. This is obviously not the case, *e.g.,* five-sixths of a half square meter were berlesed in June, 1948, and yielded only four *integer,* and five *integer* were obtained from three-sixths of a half square meter in June, 1949.

Consequently, the yield in the check experiment is well within the extremes of possible maximal yields in the two months examined. In other words, could a half square meter of fresh prairie sod have been berlesed simultaneously for the best indicated day (Table 1), then we might expect a yield of 18 *Biblo-plectus integer* on June 3, 1948 (actual yield 3 specimens per 0.08 square meter) and 24 *Biblopectus integer* on June 15, 1949 (actual yield 4 specimens per 0.08 square meter).

The yield of 22 *Biblopectus integer* from a half meter of fresh sod on June 20, 1950, therefore, may be regarded as an affirmative check on the general methods used in the population study at Peacock Prairie.

We have been concerned primarily with the small sample populations of *Biblopectus integer.* It is of interest to estimate the populations of all species of pselaphid beetles in the sod cover. If the data for the 0.08 square meter samples are used as a basis of calculation (Table 1), then the estimated square meter populations can be arrived at for the prairie sod cover. These estimates are given in Table 5, and refer to sod only; they do not include the more varied populations that frequent the lower surfaces of boards, and do not include the pselaphids berlesed from the nests of the prairie ant, *Formica cinerea neocinerea,* previously discussed.

TABLE 5. Average Monthly Population Estimates of Peacock Prairie Pselaphidae per square meter of sod cover.

Month	Total beetles taken in sod	Number of trips per month	Average per month per 0.08 sq. meter	Average per month per one sq. meter
1947				
November...	31	3	10	125
December...	7	4	2	25
1948				
January.....	2	2	1	13
February....				
March......	0	1	0	0
April........	22	6	4	50
May........	15	3	5	63
June........	5	5	1	13
July........	28	4	7	88
August.....	16	4	4	50
September..	15	5	3	38
October.....	13	4	3	38
November...	17	4	4	50
December...	3	2	1	13
1949				
January.....				
February....				
March......	5	2	2	25
April........	14	4	3	38
May........	45	4	11	138
June........	8	3	3	38
July........	4	2	2	25
August.....	1	2	0.5	6
September..	11	2	5	63
October.....	1	2	0.5	6
November...	24	5	5	63
December...	18	2	9	112
1950				
January.....	6	3	2	25
February....	1	1	1	13
March......	0	1	0	0
April........	8	2	4	50
May........	10	3	3	38

It is at the acre level that these populations seem prodigious. If these square meter averages are extrapolated to an acre, then there is the concept of an average pselaphid population of some 194,000 adult pselaphids per acre of prairie floor. Such a figure is not easily appreciated. On the other hand, the oribatoid mites and collembolans, on which pselaphid beetles are known to feed, appeared in the berlesates in far greater numbers than the pselaphid beetles plus other groups of predaceous beetles and chilopods. Consequently, the ratio of such minute herbivores to arthropod predators is consistent with the pyramid of numbers concept (Elton 1927; Park, Allee, & Shelford 1939; Williams 1941; Allee *et al.* 1949; Park, Auerbach & Corley 1950). The smallest pselaphid beetle at Peacock Prairie is *Biblopectus integer,* averaging 0.9 mm. long; the other species range upward in size to *Pilopius lacustris,* averaging 1.8 mm. long. Thus the smallest pselaphid is much larger than the majority of the oribatoid mites and collembolans, and it is much smaller and much more

abundant than the largest pselaphid. *Bibloplectus integer* is about one half the size of *Pilopius lacustris*, and about ten times more abundant.

Parallel support for such large populations is obtained from the literature. With time, our methods become more precise. This is accompanied by upward revisions of our estimates of the soil and floor populations. This general subject is reviewed in a stimulating article by Salt, Hollick, Raw & Brian (1949). These authors collected twenty samples (4 inches diameter by 12 inches deep) from the upper foot of soil in a pasture near Cambridge, England. From these samples, they extracted the astonishing total of 42,753 arthropods. As they point out, this is the equivalent of an arthropod population of some 263,000 per square meter, or about 1,068,000,000 arthropods per acre. In view of such findings, the estimated average pselaphid population per square meter at Peacock Prairie is not exceptional, especially since these averages were obtained in the course of a 31 month study and were subjected to an independent check by berlesing an entire half meter of sod simultaneously.

Recently, Strenzke (1951) collected as many as 1690 oribatoid mites from samples of humid meadow soils in northern Germany. His samples were comparable with ours at Peacock Prairie, being 0.10 square meter to a level of eight centimeters deep and the Peacock samples were 0.08 square meter to a level of seven and a half centimeters deep. Oribatid mites are abundant at Peacock Prairie, in the sod layer, and form one of the foods of pselaphid beetles (Park 1947a, b). Of especial interest is the observation of Strenzke that the populations of most of the species of oribatids studied were least numerous in late summer and in winter. In other words, the population lows of oribatid mites in northern Germany meadows soils, and of pselaphid beetles in a northern Illinois prairie remnant, were comparable. It is to be expected that the details will vary from year to year, but one would expect a general correlation in abundance between food-animals and predators in such prairies.

POPULATION TYPES AT PEACOCK PRAIRIE

There would appear to be three more or less disparate population types of pselaphid beetle populations at Peacock Prairie. The first two of these, namely the sod population and the ant nest population, need little further discussion. The third type is related to the pselaphids that are to be found on occasion clinging to the lower surfaces of boards. As is to be expected, there are few species that inhabit only a single type of habitat niche.

1. The grassland sod type. Here belong *Bibloplectus integer* and *Rhexius insculptus*. Neither species has been collected beneath boards, but have been berlesed from nests of the prairie ant, following periods of environmental stress, such as prairie fire or periods of great relative aridity. On occasion, *Reichenbachia*

subsimilis, Pselaphus fustifer, and *Pilopius lacustris* have been collected from the sod. *Rybaxis truncaticornis, Reichenbachia peregrinator* and *Batrisodes globosus* have not been so collected.

Presumably the Bibloplectus and Rhexius populations inhabit the sod and underlying soil throughout the year, moving downward in periods of relative cold or dryness and upward in periods of relative warmth or wetness, seeking refuge in ant nests only temporarily and locally under extreme conditions of weather, or of fire. They probably fly at dusk at certain times of the year, and this would appear to be the chief means of dispersal for the species involved. Neither species has been taken flying at dusk but the very closely allied *Bibloplectus ruficeps* (LeConte), a forest-dwelling species, flies abundantly at dusk in Kentucky.

This brings to mind two vertical movements in the sod: a relatively deep movement downward in winter or in arid summer, below the three inch line, with a return upward in spring and late summer to early autumn; a shorter movement upward at night with a return by day, but within the top few inches of sod. These two movements of a population, or a population fragment, are to be thought of in the most general of terms. Response is sensitive to relatively small changes in microclimate.

2. The ant nest type. Here belongs *Batrisodes globosus* and possibly *Rybaxis truncaticornis*. It is not a well-defined type at Peacock Prairie since no true myrmecophiles, e.g., species of *Adranes, Fustiger, Cercocerus,* or *Ceophyllus,* have been taken with prairie ants. These latter genera are almost always associated with rich forest, and inhabit the nests of *Lasius umbratus* or *Aphaenogaster tennesseensis* for example. Furthermore, *Batrisodes globosus* has high vagility, and is known in the Chicago area from leaf mold, log mold and tree-hole mold in forests, as well as from a wide variety of ant societies (Park 1947). This habitat niche has been discussed earlier and needs no further documentation.

3. The surface (thaw-freeze) type. On a natural prairie, boards, or their partial equivalent, logs, are not normally present. The surface is exposed to the extremes of the local environment, freezing in cold weather, baked dry in hot weather, and often flooded with rapidly melting snow and ice or after heavy rains.

The boards that were laid down at random served to protect the surface to a certain degree, their lower surfaces being relatively cool by day, warm by night, dry in wet weather and moist in dry weather. Certain species of pselaphids were beneficially stimulated by this habitat niche. Since it was an artificial one, supplied by the authors, it must be assumed that if this is a true population type, the natural equivalents are the slender stems of fallen prairie plants and accumulations of debris in depressions of the natural grassland.

Reichenbachia peregrinator and *Rybaxis truncaticornis* have not been taken in the other two habitat

niches at Peacock Prairie. Unfortunately, both species are uncommon here. Other species occur almost wholly beneath the boards, e.g., *Pselaphus fustifer* and *Pilopius lacustris*.

That this is a habitat niche with real ecological meaning may be gleaned from a single experience. A trip was taken to the prairie on January 17, 1950. The air temperature was 35° F., the soil was frozen hard. Most of the boards had their lower surfaces coated with ice, many were firmly frozen into the sod. On prying such boards free, no beetles could be seen. The boards were taken to the automobile and held up to the exhaust pipe. The motor was started and the ice began to melt away. Pilopius and Reichenbachia were then observed under the ice. When the ice had melted away the beetles began moving their appendages, and after a few moments began walking about. When the boards were removed from the flow of heat, the pselaphids slowed down, gathered their legs beneath them, with antennae placed ventrally between the legs, and assumed the position noted when they were covered by ice. Presumably such species may spend the winter at or near the surface of the sod. If this is so, then their degree of cold-hardiness must be higher than that of species that are not found in the sod surface in extreme cold.

In summary, there appear to be three types of habitat niches inhabited by pselaphids at Peacock Prairie. They are the soil-sod habitat, the ant nest habitat, and the prairie surface. Each of these habitats is inhabited by certain species of pselaphid beetles exclusively and by other species occasionally. As a consequence of the peculiarities of each habitat type, the pselaphid populations involved must adjust to different microclimates and, in the case of the ant nest, adjust to the social medium of the the hosts.

INADEQUACY OF LOCAL METEOROLOGICAL DATA

Peacock Prairie is unfenced, and on one side is adjacent to a heavily traveled highway. Under these conditions it was not feasible to set up relatively expensive recording equipment to obtain data on temperature at various critical levels in the sod and soil.

An attempt was made to correlate the frequency and amplitude of population shifts in *Bibloplectus integer* with local weather data. The attempt was unsatisfactory.

Air temperature and precipitation data were available from the Chicago Weather Bureau, and from the Glenview Naval Air Station. Both sets of data were obtained and manipulated in various ways. Although those sets of data were comparable, and the Glenview station only three miles northeast of Peacock Prairie, there was no more than a general correlation of air temperature and precipitation with Bibloplectus population fluctuations.

This suggests that continuous records of sod and soil water content and temperature at the critical level under examination are necessary. The lack of

such information is a major criticism of this report. As we become aware of such considerations (Baum, 1949), the need for precise measurement of microclimate of the stratum and habitat niche increases.

There are general correlations, of course. The relatively abundant *Bibloplectus integer* population tends to have a late vernal and an autumnal peak in adults in the sod layer. Dealing with smaller numbers of adults, other species appear to follow the same general pattern (Table 3), e.g., tend to emphasize the late vernal and the autumnal peaks. For example, the average number of adults per month for the next two most abundant species, namely, *Reichenbachia subsimilis* and *Pilopius lacustris*, show that the former had vernal peaks in April-May, 1948, and March-April, 1949, and autumnal peaks in August, 1948, and October, 1949; the latter had vernal peaks in April, 1948, and March, 1949, and an autumnal peak in October, 1948. The numbers involved are too few to do more than suggest trends.

THE LIFE CYCLE HYPOTHESES AND THE USE OF CALLOWS

It is strange that so little is known about the pselaphid life cycle. Such information would be of great value in the analysis of the Peacock Prairie populations. The family is composed of some 5,000 described species (Park 1947b) but the life history of none of the species is known. In fact, only two nearctic species have had their larval stage described (Böving & Craighead 1931). This lack of data has been discussed elsewhere (Park 1947a,b).

Without such pertinent information available, the problem must be evaluated with much less assurance. There are some suggestive data that may be used to postulate a sequence of life history events at Peacock Prairie.

If the assumption is made that the number of adults collected bears a reasonably accurate relationship to the total number of adults present at a given time, then it appears that these beetles are most abundant in the upper sod layer in the autumn and in the late spring-early summer periods. This is apparent in general when the data in Table 3 are recalculated to give the annual cycle of all species in terms of monthly averages (Fig. 5B).

From the viewpoint of comparative anatomy, the most closely allied family is the Staphylinidae. Some life history data are available for both parasitic and free-living staphylinids, and have been summarized by Balduf (1935). In free-living genera such as Philonthus and Staphylinus the oviposition period to the end of the pupa period lasts for from eleven to thirteen weeks. The life history of another staphylinid, *Nudobius pugetanus* as reported by Struble (1930) may bear on the local problem of Peacock Prairie pselaphids. *Nudobius pugetanus* overwinters both in the larval stage and in the adult stage. In the case of overwintering larvae, these enter pupation early in June of the following year and the
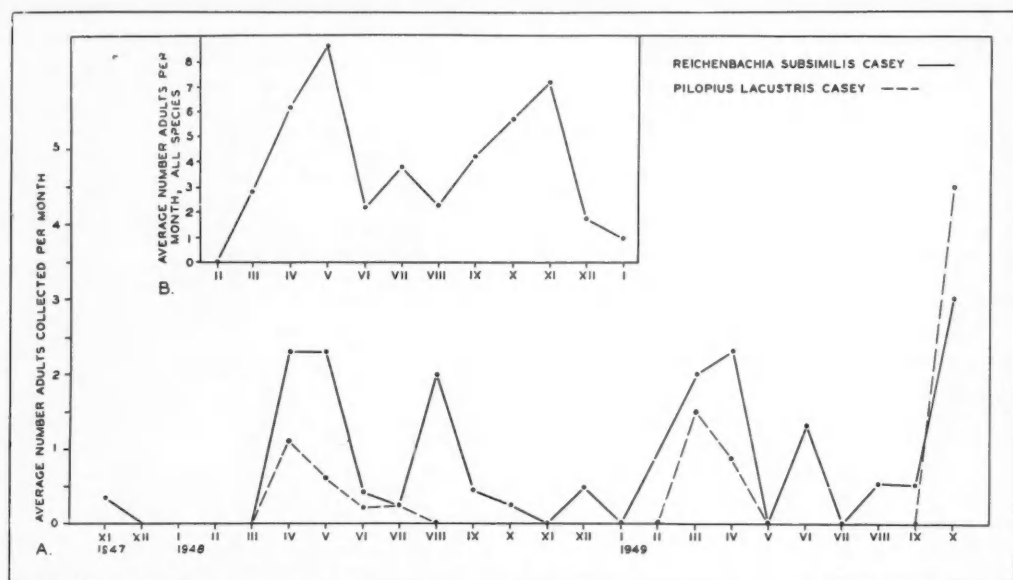
FIG. 5. A. Average number of adults per month of *Reichenbachia subsimilis* Casey and *Pilopius lacustris* Casey collected at Peacock Prairie for two years. B. Two year averages of adults of all seven species of pselaphid beetles collected per month at Peacock Prairie.

adults appear in early July and these latter mate, oviposit, and a new generation of larvae appears in the second half of August and become half grown by the time they are ready to overwinter. Second, in the case of the overwintering adults, these oviposit in early June, the larvae begin the pupal period in the middle of August and new adults emerge in early September to overwinter.

Therefore, the staphylinid *Nudobius pugetanus* has one generation per year, requiring from ten to twelve weeks for development, but differential hibernation results in two overlapping populations, so that adults appear in July and in September.

Returning to the Peacock Prairie pselaphids, evidence for the termination of the pupal period is available from a study of just-emerged adults. As with beetles in general, the just-pupated adult is relatively soft of cuticle and quite pale in color. Such light yellow pselaphids are conspicuous in species that have a dark reddish-brown color when mature. Consequently, this fact was recognized and, after September, 1948, all such specimens were noted particularly. For convenience we may differentiate the postpupal individuals as: (1) *Callow*, an individual in which neither pigmentation or sclerotization of the cuticle has been effected; (2) *Postcallow*, an individual in which pigmentation is still retarded, but in which sclerotization has become demonstrable; (3) *Imago*, an individual in which the cuticle is both pigmented and sclerotized, and presumable the individual is sexually mature. These teneral individuals collected at Peacock Prairie are given in Table 6.

TABLE 6. Callow + Postcallow pselaphids at Peacock Prairie.

Date	Biblo-plectus integer		Rhexius insculptus		Reichen-bachia subsimilis		Pselaphus fustifer	
	No.	Niche	No.	Niche	No.	Niche	No.	Niche
vii. 23.48..	1	sod						
x. 7.48..			1	sod				
x. 13.48..							1	sod
xi. 3.48..	2	sod						
xi. 10.48..			1	sod				
xi. 17.48..	1	sod						
xi. 24.48..	1	sod						
iii. 26.49..	1	sod						
iv. 9.49..	2	sod						
iv. 16.49..	1	sod						
v. 1.49..	3	sod						
v. 16.49..	16	sod						
vi. 21.49..	1	sod						
ix. 27.49..	1	sod	1	sod				
	13	ant nest						
x. 7.49..			1	ant nest	1	under board		

The scanty data in Table 6 suggest that either the trips taken to the prairie were not numerous enough at critical pupation periods, or that freshly pupated beetles were not numerous at the sod layer examined. Even so, the data on the callows and postcallows are very helpful. For example, it will be seen that there were twenty-four recently emerged

FIGURE 6. HYPOTHETICAL DIAGRAM SUGGESTING CERTAIN SEASONAL ASPECTS OF THE PSELAPHID POPULATION AT PEACOCK PRAIRIE. ONE GENERATION PER YEAR WITH TWO BROADLY OVERLAPPING POPULATIONS. STIPPLED INDIVIDUALS INDICATE IMMINENT DEATH. HIBERNATING ADULTS (WHITE) EMERGE AND MATE IN SPRING. THEIR PROGENY (WHITE LARVAE) PUPATE AND EMERGE IN AUTUMN, OVERWINTERING AS ADULTS (WHITE). HIBERNATING LARVAE (BLACK) PUPATE AND EMERGE IN SPRING (BLACK ADULTS), MATE IN SUMMER, AND THEIR PROGENY (BLACK LARVAE) HIBERNATE AS LARVAE. BASED ON ADULT FREQUENCY AND APPEARANCE OF CALLOWS. SEE FIGURE 7 FOR AN ALTERNATIVE HYPOTHESIS. SEE TEXT FOR DATA.

Fig. 6

FIGURE 7. HYPOTHETICAL DIAGRAM SUGGESTING CERTAIN SEASONAL ASPECTS OF THE PSELAPHID POPULATION AT PEACOCK PRAIRIE. OVERWINTERING BEETLES (WHITE) HIBERNATE IN DEEP SOIL OR PRAIRIE ANT NESTS. SOME ARE DESTINED TO BE WINTER-KILLED (STIPPLED). THIS GENERATION BEGINS TO EMERGE AND MATE IN EARLY SPRING, PRODUCING AN EARLY SUMMER PEAK COMPOSED OF SURVIVING BEETLES AND THE SUMMER GENERATION (BLACK). BY MIDSUMMER THE OVERWINTERING GENERATION IS DEAD AND THE SUMMER GENERATION MAY PENETRATE DEEP SOIL OR ANT NESTS TO ESCAPE SUMMER ARIDITY OR PRAIRIE FIRE. THESE BEETLES MATE TO PRODUCE THE NEXT OVERWINTERING GENERATION (WHITE) THAT BEGINS TO APPEAR IN EARLY AUTUMN. THESE TWO GENERATIONS FORM A SECOND SEASONAL PEAK OF ADULTS IN THE SOD IN LATE AUTUMN. WITH ONSET OF WINTER, THE SUMMER GENERATION HAVING DIED (STIPPLED), THE SECOND GENERATION REPEATS THE CYCLE. BASED ON ADULT FREQUENCY AND APPEARANCE OF CALLOWS. SEE TEXT FOR DATA.

Fig. 7

adults in the autumnal period, between September 27 and November 24; whereas, there were twenty-three recently emerged adults in the vernal period, between March 26 and May 16. All but two of the callows fall into one or the other of these periods.

When these two groups of callows and postcallows are compared with the average monthly collections of adults for all species at Peacock Prairie (Fig. 5B), it will be seen that they are congruent both in frequency and amplitude. With this in mind, there appear to be two hypotheses that are tenable.

Hypothesis I. At least some of the species of pse-

laphids at Peacock Prairie have one generation per year, but with two broadly overlapping populations so that adults and larvae overwinter (Fig. 6).

In this case, the overwintering adults emerge from hibernation in the spring, mate and die during the course of the summer. Their progeny pupate in the autumn and overwinter as adults.

The overwintering larvae pupate in the spring, the resulting adults mate, and die during late autumn and winter. Their progeny overwinter as larvae.

Consequently, the overwintering larvae would pupate in the spring and the vernal peak would be composed of overwintering adults and spring pupation adults. In autumn, the larvae produced in the spring (as a consequence of mating by overwintering adults only, or by mating of these with just-pupated adults) pupate. The autumn adult peak would be composed

FIG. 8. *Bibloplectus integer* (LeConte). 1. Dorsal aspect of male, 70x. 2. Eleventh (distal) antennal segment, under oil at 920x. Note the normal setae, and the alpha cones with large core. 3. Stereogram of distal antennal segment, to show the symmetrical disposition of the eight alpha cones. 4. Left elytron, from lateral view, to show pubescent subhumeral fovea, and longitudinal sulcus, 70x. 5. Posterior sternites of male, to show slightly asymmetrical, oval, penial plate, 70x. 6. Posterior sternites of female, 70x.

of surviving spring-pupated adults and autumn-pupated adults. At onset of winter, the spring-pupated adults die and leave an overwintering population of autumn-pupated adults and the larvae produced by the summer mating of spring-pupated adults.

One interpretation of this first hypothesis would allow little chance for the two populations to interbreed. The difficulty with this interpretation is to imagine how such a situation could arise initially, as there would be two populations of the same species in which individuals were maturing sexually at differing times of the year. One explanation could be that the prairie had an initial population that overwintered as larvae, and that, at some time, overwintering adults from another part of the species range emigrated to the prairie in the autumn.

A more tempting interpretation of this first hypothesis is that there is no seasonal barrier of differential mating, but that adults of the vernal peak freely interbreed to produce the summer progeny.

Hypothesis II. At least some of the species of pselaphids at Peacock Prairie have two generations a year, with hibernating adults but no hibernating larvae.

In this case, overwintering adults are partially winter-killed, but the survivors emerge in the spring and mate. The vernal peak is composed of the survivors of the overwintering generation and the adults resulting from the early spring mating. By midsummer the overwintering adults are dead. The spring generation mates, and their progeny pupate in the autumn. The autumnal peak is composed of the surviving adults of the spring generation and the autumn generation. The spring generation adults die in late autumn and winter, and the autumn generation adults hibernate to continue the cycle the following year.

In this hypothesis there is no isolation of gene flow between individuals, as one generation gives rise to the next, in step with the reproductive cycle of the species. The difficulty with this hypothesis is that the spring generation would have to be much more accelerated than the autumn generation in order to keep within the apparent limits set by the peaks of callows and peaks of adult abundance. If we are to keep in mind the rather well-established effect of temperature upon developmental rate, we should expect that the spring generation would be retarded and the autumn generation accelerated.

The minute size and probably predaceous habits are thought to be more in favor of this second hypothesis, which is depicted in very diagrammatic form in Fig. 7.

Only future research will show whether either of these hypotheses is tenable in whole, in part, or in combination. For example, we may be concerned with some species that are parasitic in the egg or early larval instars, or that are ovoviviparous, whereas other species may have the usual type of life cycle in Coleoptera.

Since the species discussed here are either absent or

scarce in the upper sod layer during winter, both hypotheses assume that the insects hibernate in the sod below the three inch line, or in ant nests, or belong to the thaw-freeze surface group discussed earlier.

It is possible that instead of hibernation in the prairie some of the species move into more protected forest floors for overwintering and return to the prairie the following spring. This possibility is not favorably viewed for several reasons. The record of teneral individuals (callows and postcallows) suggests that these delicate and freshly pupated insects have undergone metamorphosis in the prairie sod, and emigration into the prairie in their condition is not feasible. There is also evidence that the Peacock Prairie populations may migrate vertically into deeper sod levels at the onset of colder weather. This evidence, drawn from literature, is general and specific. For example, Dowdy (1944) found that both the downward hibernal and upward vernal movement of invertebrates of floor and subterranean strata took place in a variety of soils, and that such movements were close to the temperature overturns and usually coincident with them. More immediately relevant is the datum of Thompson (1924), who found a specimen of the pselaphid *Euplectus brunneus* in a Welsh meadow sod at three inches in July, and another specimen of this species at between three and nine inches in February in the same meadow.

SUMMARY

Three additional species of pselaphid beetles are reported from Peacock Prairie, near Evanston, Cook County, Illinois, bringing the known fauna to eight species.

Of these three additional species, one, *Batrisodes globosus*, was collected three times from berlesed samples of nests of the prairie ant, *Formica cinerea neocinerea*. This is the first record of this well-known inquiline with this species of host. The other two species, *Rybaxis truncaticornis* and *Reichenbachia peregrinator,* have known distributions westwards into the Great Plains, and are the second and third species that give additional support to the Prairie Peninsula Hypothesis.

A key to both sexes of these eight species is provided.

Following a grass fire, it was noted that the nests of *Formica neocinerea* harbored large numbers of the non-inquilinous *Bibloplectus integer* as well as other typical prairie sod arthropod inhabitants. It is suggested that (a) forest-inhabiting pselaphids may utilize ant nests to invade grassland, and (b) such ant nests may be reservoirs of prairie pselaphids during periods of winter cold, summer aridity, and prairie fires.

The pselaphid fauna of the prairie was studied quantitatively. Eighty-five trips were made to the prairie over a period of about two and a half years, between November, 1947, and May, 1950. In this period 606 pselaphids were collected. Of these, 326 were berlesed from sod samples; 197 were collected from beneath boards, and 83 were berlesed from ant nests. The minute *Bibloplectus integer* composed 56 per cent of all pselaphids collected.

The eight species exhibit differential niche distribution and the fauna is divisible into three population types. The grassland sod type includes *Bibloplectus integer* and *Rhexius insculptus;* the thaw-freeze surface type includes *Reichenbachia peregrinator, Rybaxis truncaticornis,* and *Pilopius lacustris;* the ant-nest type is represented by *Batrisodes globosus.* Rybaxis may also enter ant nests, and *Pselaphus fustifer* and *Reichenbachia subsimilis* may be found in both of the first two habitat niches.

These eight species were analysed in terms of average number of each species per trip, per month, per habitat niche per month, per 0.08 square meter per month, and per square meter per month. The population cycle of *Bibloplectus integer* was used especially since the species is relatively abundant at the prairie. In general it was found that the whole fauna tended to have a spring to early summer peak, a late summer to early autumn low, an autumn peak, and a winter low.

Square meter sod populations, estimated from small samples berlesed, varied from no pselaphids to a maximum of 138. The small samples were subjected to an independent check. After the thirty-one-month period was completed, a half square meter was berlesed simultaneously. This check sample, collected June 20, 1950, yielded 22 *Bibloplectus integer,* and is an affirmative check on the general methods used since the expected yield for June 3, 1948, was 18, and for June 15, 1949, was 24 of the beetles.

Acre populations extrapolated from the square meter figures seem very large, *e.g.,* 194,000 as an average figure of pselaphids per acre at Peacock Prairie. Such figures are smaller than those for food-animals present, *e.g.,* acarina and collembola, and are in general accord with meadow sod arthropod estimates in the literature.

Freshly pupated pselaphids ("callows") are light in color and weakly sclerotized. Of 49 callows obtained, 23 were in the vernal peak, and 24 in the autumnal peak.

Since the life history is unknown for any species of Pselaphidae, two alternative life cycle hypotheses are suggested, taking into account the vernal and autumnal peaks of adult abundance and callow distribution. One hypothesis suggests one generation per year, with two broadly overlapping populations, one of which overwinters in the adult stage and one overwinters in the larval stage. A second hypothesis suggests two generations a year, in which a spring generation gives rise to an autumn generation, this latter overwintering in the adult stage. Neither hypothesis is free from criticism, and await future accumulation of information.

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STUDIES ON THE LIFE-HISTORY OF *SYMPHORICARPOS OCCIDENTALIS* HOOK. IN MINNESOTA

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TABLE OF CONTENTS

INTRODUCTION

The investigation reported below concerns the ecology of the widely distributed shrub, *Symphoricarpos occidentalis* Hook., commonly known as wolfberry or western snowberry. The objectives were twofold: First, to survey the distribution, abundance, variation, and economic relations of the species throughout its total range, this being accomplished mainly by a review of the literature, supplemented with some original observations within Minnesota; and second, to examine in some detail for a few Minnesota localities the ecological life-history of the shrub. The second objective received the major emphasis.

It is a pleasure to acknowledge the advice, information, and aid given by many individuals at the University of Minnesota and elsewhere. I am particularly indebted to Dr. D. B. Lawrence, my major advisor; Dr. H. L. Hansen, my minor advisor; Dr. J. W. Moore, Dr. C. M. Christensen, Dr. E. F. Cook, and Dr. J. R. Beer, who are responsible for identifications of seed plants, fungi, insects, and mammals, respectively; Dr. E. W. Tisdale, Miss F. Flemion, Dr. P. R. McMiller, and Mr. P. O. Rudolf for useful information; Mr. F. L. McGuire, my wife, Mrs. J. Siron, and Mrs. G. Lee for invaluable assistance during the course of the investigation; and to Mr. C. Brand, who established the fellowship under which the writer worked during 1949-1950.

CLASSIFICATION

The genus *Symphoricarpos*, belonging to the Caprifoliaceae, is composed of woody shrubs, sixteen of which are described from North America and one from China. The group is probably of considerable antiquity (Clements 1916). Two species of the fossil form genus *Symphoricarpophyllum* have been obtained from the Eocene in Alberta (Knowlton 1919).

The most recent taxonomic monograph of the genus is that by Jones (1940), who accepts as valid the name *S. occidentalis* established by Hooker in 1833. Western snowberry is the common name for this species approved by some authorities (Kelsey & Dayton 1942, Saskatchewan Advisory Weed Council 1950), but wolfberry appears to be more commonly used in Minnesota. The name western snowberry would seem to be misleading, for the species is actually more eastern in its range than are the great majority of the North American species of *Symphoricarpos*. Other occasionally used names include buckbrush, badger-brush, and chicken-willow.

Wolfberry is an erect shrub 30 to 100 cm or more tall (Fig. 4), a deciduous nanophanerophyte according to the life-form classification of Raunkiaer (1934). Spreading by rhizomes the shrub usually forms colonies from a meter or two to over 200 meters in diameter (Fig. 1, 2, 3), this habit being its most distinctive feature. The opposite and ovate leaves are 3 to 5 cm or more long. The flowers are moder-

ately large, white or pink, and are borne near the tips of the current season's shoots in dense clusters. The fruits are nearly spherical berry-like drupes, yellowish-white at maturity. When flowering specimens are available wolfberry may be readily distinguished from all other species of *Symphoricarpos* (Jones 1940). The short campanulate corolla places it in the subgenus EUSYMPHORICARPOS, while the slightly exserted, rather than included, style and stamens separate *S. occidentalis* from the remaining species. The only other species within the genus occurring naturally in Minnesota is *S. albus* (L.) Blake,

which is readily distinguished from wolfberry even when flowers or fruits are absent. Sax & Kribs (1930) state that natural species hybrids occur in the genus *Symphoricarpos* but do not mention the species concerned. No possible hybrids, however, were observed between *S. occidentalis* and *S. albus* in Minnesota.

FIG. 3. October aspect of a portion of a colony growing in a dense bluegrass *(Poa pratensis)* sod at Station 4.

FIG. 1. June aspect of extensive colonies of Symphoricarpos on a south facing slope in a lightly grazed pasture in south-central Minnesota (Station 5).

FIG. 2. Winter aspect of Symphoricarpos colonies bordering the edge of a bur oak *(Quercus macrocarpa)* forest on an ungrazed south facing bluff near Minneapolis (Station 4). Meter stick at left.

FIG. 4. October aspect of two fruiting stems of average vigor near the edge of the colony illustrated in Fig. 3, showing the usual growth habit. The stems are connected by a rhizome, the stem on the left being 3 years old and the one at the right 5 years old. The height of the older stem is 81 cm.

Jones (1940) does not recognize any varieties of *S. occidentalis*, although two had been previously proposed, and states that wolfberry appears to be very uniform throughout its range. Some morphological differences almost certainly attributable to genetic variation were observed by the writer among both seedlings and mature plants. Most of the variation observed within Minnesota, however, appeared to result from environmental differences, but transplant experiments are needed to prove this point. Ecotypic or clinal differentiation of *S. occidentalis* is quite possibly present even within Minnesota alone.

ECONOMICS

Indians made limited use of *S. occidentalis* for food, arrow shafts, brooms, and for treatment of certain eye diseases (Blankinship 1905; Gilmore 1911-12). At the present time wolfberry has both its positive and negative economic aspects (Van Dersal 1938). The species is generally considered to be a serious weed in pastures, particularly in the eastern parts of its range (Pound & Clements 1898; Dr. A. H. Larson and Mr. I. J. Nygard, communications). On the plains and in the aspen parklands of Canada, wolfberry appears to be rather uniformly unpalatable to livestock, and does not seem to be eaten to any extent even where forage is scarce (Dr. E. W. Tisdale, communication). On the other hand, in the western part of its range, as in Utah, this does not seem to be generally true for the species is here considered an important and nonpoisonous winter cattle browse (Dayton 1931).

Observations in Minnesota suggest that there is here a limited amount of browsing of the dried fruits and young twigs of *S. occidentalis* by livestock, probably almost entirely in winter. Because of the shrub's apparent tendency to spread in Minnesota under conditions of intense grazing, however, major portions of large pastures are frequently rendered relatively useless by the dense colonies, and its usual appraisal as a serious pasture weed is certainly justified in many Minnesota localities. The responses of the shrub to grazing and control treatments are discussed in the section on resistance.

Wolfberry is of considerable wildlife value in Minnesota and elsewhere. The fact that the shrub is one of the few which forms dense protective colonies on the open prairie probably renders it of relatively greater wildlife cover value than would be the case if it were restricted to wooded regions. Game birds for which leaves or fruits of *S. occidentalis* are an important food include the greater prairie chicken *(Tympanuchus cupido pinnatus)*, the ring-neck pheasant *(Phasianus colchicus torquatus)*, the sharp-tailed grouse *(Pedioecetes phasianellus campestris)*, and certain ducks (Metcalf 1931; Van Dersal 1938; Swenk & Selko 1938; Krefting & Roe 1949). In the Black Hills of South Dakota *S. occidentalis* was found to be among the most important winter foods of whitetail deer *(Odocoileus virginianus macrourus)* and mule deer *(O. hemionus)* by Hill & Harris

(1943). Although no birds were noted feeding on the shrub during the period of study by the writer, the seeds were observed to be an important food of mice, and the stems and fruits are occasionally browsed by rabbits.

Wolfberry is an important honey plant where it is abundant (Pellett 1923; Van Dersal 1938). Because of its aggressive colonizing habit and its tolerance of infertile soils and drought, the shrub is rated highly for erosion-control (Bennett 1939). The earliest record of its cultivation as an ornamental is 1880 (Rehder 1940), but other species of *Symphoricarpos* are more attractive for this purpose.

DISTRIBUTION

RANGE

Wolfberry is one of the characteristic and abundant shrubs of the northern great plains and fringing forested areas of the United States and Canada, extending over the continental divide and almost reaching the Pacific Coast in Washington and British Columbia (Fig. 5). Fernald (1950) reports that the shrub is now "naturalized" in New England and Pennsylvania. In the western mountains the species ranges up to 7200 ft. elevation in Montana (Rydberg 1900) and to 9000 ft. in Utah (R. Zon, quoted by Clements 1920). In the northern plains region *S.*
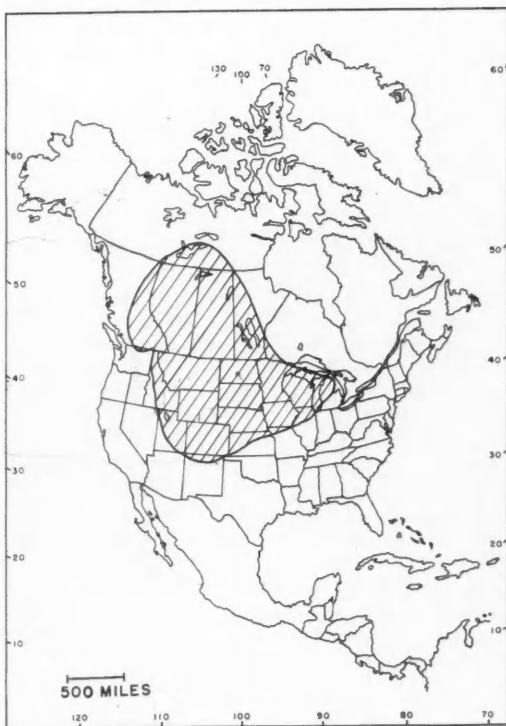
FIG. 5. Provisional range map of *S. occidentalis*, excluding areas where it is known to be only naturalized or cultivated.

occidentalis appears to be the most abundant species of its genus, but tends to be replaced by *S. orbiculatus* toward the south and southeast, by *S. oreophilus, S. rivularis*, and other species west of the plains, and by *S. albus* north and east of the prairies (Jones 1940). Essentially nothing is known of the migrations and range fluctuations of wolfberry during post-glacial times, although Harshberger (1911) has presented some conjectures on the subject.

The distribution of *S. occidentalis* in Minnesota is illustrated in Fig. 6. Observation suggests that the species is probably present in all the counties south and west of the Mississippi River, and it is not at all unlikely that wolfberry is present in all the counties within the state. Observations by the writer confirm the earlier ones of Upham (1884) and Rosendahl & Butters (1928) that the species is common in and bordering the Red River Valley in the northwestern part of the state, becoming progressively less frequent eastward. The shrub is perhaps even more abundant in the southern half of the state, except in the unshaded areas of Fig. 6.
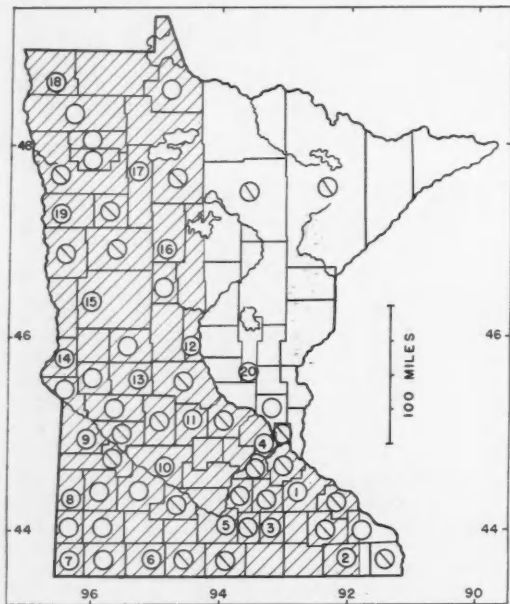
FIG. 6. Distribution of *S. occidentalis* in Minnesota. Numbered circles mark stations closely studied by the writer; ● represent counties where no stations were established but which are represented by specimens of *S. occidentalis* in the University of Minnesota herbarium; ○ represent sight records only. The species is relatively rare in the non-cross hatched portions of the map.

COMMUNITIES

As is to be expected of most widely ranging species, *S. occidentalis* occurs in a great variety of communities and vegetation types. Within much of its range the species is a characteristic component of the shrub layer of open woods, of the forest-prairie

ecotone, of chaparral, of pastures and disturbed areas, and of open prairie and plains. Although *S. occidentalis* occurs in certain presumed climax communities, such as some grassland and chaparral types, it is very common in seral communities on immature soils, and in the transition zone between forest and grassland. The fact that wolfberry is one of the few woody plants which can successfully invade grassland (by means of rhizomes) in such quantities as to shade out the grasses and permit invasion by trees is perhaps the shrub's most striking successional role. In Canada the invading tree is *Populus tremuloides** (Moss 1932) while in Iowa and Nebraska it is primarily *Quercus macrocarpa* (Weaver 1919, Aikman 1928).

In various parts of its range, exclusive of Minnesota, *S. occidentalis* is reported to occur bordering groves or in open woods of *Populus tremuloides, Quercus macrocarpa, Fraxinus pennsylvanica* v. *subintegerrima, Ulmus americana, Acer negundo, Tilia americana, Celtis occidentalis*, and other hardwoods. West of the plains wolfberry may be associated with coniferous forests of *Pinus ponderosa* v. *scopulorum, P. contorta* v. *latifolia*, and *Pseudotsuga taxifolia*. Common shrub associates are *Eleagnus commutata, Xanthoxylum americanum, Shepherdia* spp, *Amelanchier* spp, *Prunus* spp, *Rhus* spp, *Corylus* spp, *Rosa* spp, and *Symphoricarpos* spp. The brush communities, in addition to bordering the forest edge or forming chaparral, may occur locally in favorable spots in a number of grassland types. References to communities or vegetation types in which *S. occidentalis* occurs may be found in the following works: *General:* Clements 1920; Rydberg 1932; Weaver & Fitzpatrick 1934; Aikman 1935; U. S. Forest Service 1948; Fernald 1950. *Canada:* Macoun 1884; Jackson 1924; Moss 1932, 1944; Raup 1936; Clarke, Campbell, & Campbell 1942; Clarke, Tisdale, & Skoglund 1943; Lowe 1943; Mitchell, Moss, & Clayton 1944; Fraser & Russel 1944; Moss & Campbell 1947; Coupland 1950. *North Dakota:* Bergman 1912; Metcalf 1931; Hanson & Whitman 1938. *South Dakota:* Hayward 1928; Over 1932; Tolstead 1941; Larson & Whitman 1942. *Nebraska:* Pound & Clements 1898; Pool 1914; Steiger 1930; Weaver and Bruner 1948. *Kansas:* Gates 1940. *Iowa:* Fink 1897; Fitzpatrick 1897, 1899; Cratty 1904; Aikman 1928. *Wyoming:* Nelson 1896. *Montana:* Standley 1921.

There are few references to the community relations of *S. occidentalis* in Minnesota. Rosendahl & Butters (1928) describe the species as being common to the prairie and hardwood districts and as being one of the few woody plants which grows freely out on the open prairie, and MacMillan (1892, 1899) and Jones (1948) observed wolfberry at the forest edge and in open woods. Ewing (1924) found the shrub in both hydrarch and xerarch successions. A brief survey of the distribution and associates of wolfberry in Minnesota was made by the writer, the main stations examined being numbered in Fig. 6. The shrub

* The nomenclature in the subsequent discussion corresponds to that of Fernald (1950).

was frequently found to be abundant in open decidu-
ous woods, as a narrow fringe along their margins,
and even more commonly out in the open. The de-
ciduous forests with which *S. occidentalis* is often
associated include both upland and lowland species,
especially *Ulmus americana, Acer negundo, Quercus
macrocarpa,* and *Fraxinus pennsylvanica* v. *subinte-
gerrima,* listed in order of decreasing frequency. At
only one locality examined (Station 16) did wolfberry
occur in or adjacent to coniferous woods *(Pinus
banksiana).* Here, however, the available evidence
strongly suggests that the area has been recently
invaded by the pines, and that the shrub remains
essentially as a relict.

Wolfberry is also common in the originally non-
forested regions of the state, and is particularly
characteristic of present or former pastures through-
out Minnesota. The species is frequent in the heter-
ogeneous but at least partially protected communities
of fence rows, railway right-of-ways, roadsides, steep
bluffs, and ungrazed woodlots or grassland. The only
ubiquitous associate of the shrub in Minnesota, oc-
curring as a layer dominant within almost all col-
onies examined, is bluegrass *(Poa pratensis).* Weaver
& Fitzpatrick (1934) have noted that this grass is
the last to die out under invading colonies of *S. occi-
dentalis.* In addition to bluegrass, the ruderal herbs
Agropyron repens, Ambrosia artemisifolia v. *elatior,
Asclepias syriaca, Vicia americana,* and *Achillea
lanulosa* occurred within wolfberry clumps at 45 to
75% of the stations. Shrubs are less common within
the colonies, but *Rhus radicans* was present in half
of them. *Parthenocissus quinquefolia* and *Rosa
blanda* each showed presence values of 40%, and
Xanthoxylum americanum was present within wolf-
berry clumps at 30% of the stations.

HABITATS

CLIMATE

Symphoricarpos occidentalis is a species which
occurs naturally only in climates of a strongly conti-
nental type, that is, those in which the seasonal tem-
perature ranges are extreme and the precipitation
light to moderate. Beyond this statement, however, it
is difficult to generalize, for the range limits of the
shrub show no close correlation with the boundaries
of any recognized climatic type. The variety of cli-
matic conditions which wolfberry endures within its
natural range is indicated by comparing the data in
Table 1 for stations close to the periphery of its dis-
tribution in North America. Considerable variations
in temperature and precipitation occur even within
the natural range of the shrub in Minnesota (Table
1). Wolfberry is scarcest in those regions of the state
where the precipitation is highest, the northeastern
and southeastern sections. These are the areas which
originally were most densely forested, and the forest
competition rather than any direct climatic factor
may be the excluding agent.

Probably the most common situation of *S. occi-
dentalis* in regard to light intensity is full or nearly

TABLE 1. Climatic data for stations near the periphery
of the natural range of *S. occidentalis* in Minnesota and
in North America. Data are from U. S. Department of
Agriculture (1941).

Station		TEMPERATURE (°F)				MEAN PRECIPITATION (inches)				
		Means		Extremes						
		January	July	Maximum	Minimum	December-February	March-May	June-August	September-November	Annual
Minnesota	Northeast Virginia	6.8	66.8	103	−45	2.52	5.55	10.91	7.06	26.04
	Northwest Hallock	0.8	67.5	109	−51	1.73	4.48	8.82	4.58	19.61
	Southeast Caledonia	14.6	71.2	104	−35	3.28	8.82	12.96	8.50	33.56
	Southwest Pipestone	13.5	72.7	108	−40	1.66	6.00	10.29	5.45	23.40
Colorado	Southeast Two Buttes	31.1	76.6	111	−26	1.24	4.17	5.66	2.55	13.62
Washington	North-central Conconully	20.8	66.6	109	−29	4.24	3.30	3.06	3.76	14.36
Michigan	Northeast Oscoda	17.9	66.8	112	−47	4.34	6.91	8.62	7.46	27.23
Alberta	Northern Chipewyan	−12.7	59.4	93	−58	2.02	2.20	5.30	3.07	12.59

full sun. Since the shrub frequents the forest border,
however, it is often found under partial shade, and
occasionally in dense shade. Light readings made at
noon on a clear day in June showed only 5% of
full sun in a relatively deeply shaded Symphoricarpos
habitat, as measured with a photoelectric meter on
the reflection from a square foot white cardboard.

TOPOGRAPHY

In the more humid parts of its range, *S. occiden-
talis* occurs most abundantly on the drier topographic
sites, as on exposed bluffs, open hillsides, and south
and west facing slopes, probably largely as a con-
sequence of lesser competition from taller vegetation
in these locations. In drier regions wolfberry occurs
more commonly on the moister sites, as in depressions
and ravines, near the shores of lakes and sloughs,
along stream banks and floodplains, at the base of
steep slopes where runoff is received from above or
where snowdrifts accumulate, and on north or east
facing slopes. Publications which mention the oc-
currence of *S. occidentalis* in relation to topography,
slope, exposure, or moisture include the following:
General: Rydberg 1932; U. S. Forest Service 1936;
Van Dersal 1938; Jones 1940; Fernald 1950. *Can-
ada:* Moss 1932; Fraser & Russel 1944. *North Da-
kota:* Bell 1907-10; Bergman 1912; Metcalf 1931;
Hanson & Whitman 1938. *South Dakota:* Hayward
1928. *Nebraska:* Pound & Clements 1898; Bates &
Pierce 1913; Pool 1914; Steiger 1930; Weaver &

Bruner 1948. *Kansas:* Hitchcock 1896; Gates 1940. *Iowa:* Fitzpatrick 1899; Cratty 1904; Greene 1907. *Missouri:* Bush 1895. *Illinois:* Jones 1945. *Michigan:* Dodge 1921. *Colorado:* Cary 1911. *Wyoming:* Nelson 1896. *Montana:* Standley 1921.

Observations by MacMillan (1899) and the writer in Minnesota indicate that wolfberry does not demonstrate any consistent topographic restrictions, probably largely owing to the fact the state is climatically transitional and exhibits a wide variety of soils. At Station 8 strong preference for north facing slopes, ravines and pockets, and bases of large rolling hills was evidenced, and at Station 11 wolfberry was abundant on 45° northeast facing railway embankments, but was rare on the corresponding southwest facing side. Relatively moist alluvial stream flats were occupied at Stations 2, 3, 5, 7, and 9, frequently in addition to the drier adjacent hill slopes. On the other hand, at Stations 1, 2, 4 (Fig. 2), 5 (Fig. 1), 10, and 16 most of the colonies occurred on relatively dry south facing slopes or on tops of bluffs or hills.

SOIL

These descriptions of the wide geographic range and great variety of communities and topographic situations in which *S. occidentalis* occurs suggest that generalizations concerning soil restrictions of the species will not be many. The shrub is apparently common on both mature grassland and some mature forest soils, as well as on immature alluviums and lithosols. Wolfberry has not been reported on saline or alkali soils, nor on very acid or organic substrates. In many parts of its range the shrub is present on soils which vary from infertile sand or rocky substrates through rich loams to compact clay. Publications which refer to soil occupied by *S. occidentalis* in other respects than just the topographic or moisture relations include the following: *Canada:* Raup 1936; Mitchell, Moss & Clayton 1944; Moss 1944. *North Dakota:* Bell 1907-10; Hanson & Whitman 1938; *South Dakota:* Larson & Whitman 1942. *Nebraska:* Pound & Clements 1898; Pool 1914; Weaver & Bruner 1948. *Missouri:* Bush 1895; Palmer & Steyermark 1935. *Wyoming:* Nelson 1896.

A brief survey of the soils occupied by *S. occidentalis* in Minnesota was made at the twenty localities numbered in Fig. 6. Surface 10 cm samples were collected and profile pits dug near the centers of colonies, following which the soils were air dried and glass-electrode pH measurements and Bouyoucos (1936) texture analyses made. Presence of free carbonates was tested with dilute HCl. The results of the texture and pH measurements on the surface soils are presented in Table 2. It is seen that although the species grows on sands or sandy loams at thirteen of the twenty stations the shrub is by no means restricted to these soils in the state. With the exception of Station 2, however, all of the colonies on the heavier soils occurred in the drier western one-third of the state. Only one locality (Station 14) showed a surface soil heavier than loam. It seems probable that the apparent preference of wolfberry

for the lighter soils in the eastern part of the state may result at least in part from the lesser competition with taller shrubs and trees on such soils, compared to the more fertile loams. Dr. E. W. Tisdale (communication) has observed that *S. occidentalis* is largely confined to permeable sandy soils in the drier parts of the plains. This compensation for low precipitation, however, appears to be uncommon in western Minnesota where the species is characteristic of heavier soils, but this part of the state is still relatively moist compared to the plains region . Further-

TABLE 2. Texture, pH, and parent material of surface soils from colonies of *S. occidentalis* at the twenty localities in Minnesota numbered in Fig. 6.

Station	pH	Percent total sands (2.0-0.05 mm)	Percent total silt (0.05-0.002 mm)	Percent total clay (0.002-0 mm)	Textural class name (Davis and Bennett 1927)	Parent material
		TEXTURE ANALYSIS				
1......	6.5	72.2	15.8	12.0	sandy loam	Kansan gray drift
2......	7.6	42.6	46.6	10.8	loam	alluvium
3......	6.8	60.0	29.0	11.0	sandy loam	outwash
4......	6.3	82.0	10.7	7.3	loamy sand	outwash
5......	6.6	50.8	35.4	13.8	sandy loam	Wisconsin gray drift
6......	8.4	65.2	19.0	15.8	sandy loam	Wisconsin gray drift
7......	8.1	36.8	46.6	16.6	loam	alluvium
8......	6.8	37.2	44.8	18.0	loam	Iowan gray drift
9......	8.4	55.6	30.6	13.8	sandy loam	alluvium
10......	7.0	68.2	21.0	10.8	sandy loam	Pre-Cambrian rock
11......	6.8	79.8	12.0	8.2	sandy loam	Wisconsin gray drift
12......	6.2	70.8	22.4	6.8	sandy loam	outwash
13......	6.7	40.0	46.6	13.4	loam	outwash
14......	6.7	33.2	43.4	23.4	clay loam	lacustrine clay
15......	6.8	71.2	23.8	5.0	sandy loam	Wisconsin gray drift
16......	6.4	76.8	15.6	7.6	sandy loam	outwash
17......	6.7	53.2	36.8	10.0	sandy loam	Wisconsin gray drift
18......	7.5	46.8	34.0	19.2	loam	lacustrine clay
19......	8.1	42.0	45.6	12.4	loam	lacustrine silt
20......	6.1	85.0	10.9	4.1	loamy sand	outwash or dune

more, the factor compensating for lower precipitation at several of the stations near the drier western border appeared to be the relatively high water table on the stream flats where the shrub commonly occurs.

The surface soil at seven of the twenty localities had a pH of 7.0 or above and four stations gave a pH reading of over 8.0, free carbonates being present in these latter four soils. Although several additional soils had free carbonates only at deeper levels, a number showed a complete absence of carbonates throughout the profile, and surface soils were only pH 6.1 at one locality. Consequently, although the species is absent from soils which are more than slightly acid, it probably cannot be considered strongly calciphilic in Minnesota although it has been considered as such in Missouri by Palmer & Steyermark (1935).

The soil profiles are of great variety. None of them, however, are either highly acid at any depth or very podzolized, and free carbonates are present at least in the subsoil in about half of the soils examined. The texture ranges from sand to clay loam

at the surface to stiff clay just below the surface soil, but well developed hardpans are absent. The great majority are immature soils. There appears to be little consistent correlation of the distribution of *S. occidentalis* in Minnesota and the geologic substratum, as is suggested by the wide range of parent materials listed in Table 2.

Observations by the writer and Ewing (1924) suggest that *S. occidentalis* tolerates rather poorly drained sites, although it more frequently grows on well drained soils in Minnesota. The species has not been observed by the writer, however, to occur on areas exhibiting a permanent water table very close to the surface. The organic matter content appears to vary as widely among soils occupied by wolfberry as it does among any mineral soils observed in Minnesota. The species has not been reported to occur on even drained and circumneutral peats or mucks, however. Observations suggest that soil fertility affects the distribution of the species in Minnesota primarily by influencing the type of competitive vegetation, rather than by acting upon possible narrow tolerances of the shrub itself.

FIRE

The factor of fire has probably been of importance within the range of *S. occidentalis* for an indefinite period. It is likely that the encroachment of the forest and its shrub border upon the grassland, as described above, is at least partially the consequence of the reduction of prairie fires following white settlement. Fire probably influences the distribution of wolfberry both directly through its action on the plants themselves and indirectly by controlling the type of competitive vegetation, as mentioned in a succeeding section.

LIFE-HISTORY

SEED STAGE

DISPERSAL

The fruit of Symphoricarpos is a berry-like drupe containing two seed-like nutlets (Pfeiffer 1934). The records of wildlife utilization of fruits referred to above suggest that at least some birds and mammals function in dissemination of the species, and indeed, it would be very difficult to account for the present wide distribution of the species without assuming at least some bird or mammal dispersal. The fresh fruits are very astringent, and observations by the writer and other sources (Dayton 1931; Hill & Harris 1943; Krefting & Roe 1949) show that certain mammals and birds appear to prefer the dried fruits which remain attached to the shrubs. Rabbits and mice, both of which eat the dried fruits, are probably relatively ineffective in dispersal. Only the macerated fragments of Symphoricarpos nutlets were recovered from rabbit pellets by the writer, and mice split open each nutlet and travel but very short distances. Livestock and the large indigenous herbivores may be important dispersal agents, for it is probable that at least some nutlets are capable of passing unharmed

through the digestive tracts of these animals. Fried (1938) has reported that nutlets of wolfberry readily pass through the digestive tract of the ring-necked pheasant, while Krefting & Roe (1949) report finding the nutlets of *S. occidentalis* in viable condition in the droppings of sharp-tailed grouse.

A brief test of the durability of wolfberry nutlets was made by the writer through feeding nutlets to a domesticated chicken. Only 10.7% of 150 nutlets force-fed the bird in gelatin capsules were passed intact. Thus it seems that passage of intact wolfberry nutlets through the digestive tract of at least some birds can reach a fairly low level, but that a certain proportion will probably survive.

Studies of the normal time of falling of the fruits, barring use by animals, were made on several stems of a colony near Minneapolis (Stat. 4, Fig. 6). Counts of fruits were made at weekly intervals except in winter, the results for four representative plants being presented in Fig. 7. Apparently no abscission layer is formed at all in the fruit pedicel, slow disintegration of which eventually permits the fruit to fall. No evidence of mammal or bird feeding was observed except on the 1948 crop of Plant C, the rapid drop-off after September 18 being due to mice.
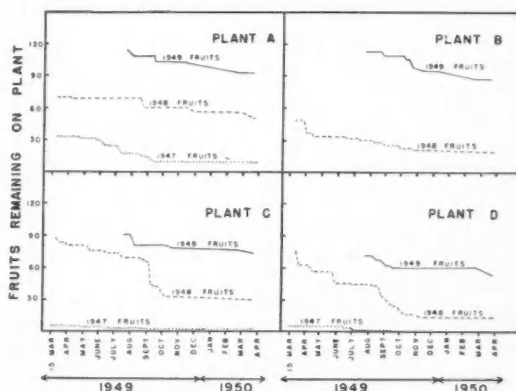
FIG. 7. Fruit counts of four stems during 1949 and 1950 at Station 4. The year the crop was matured is given for each stem.

There is comparatively little correlation of fruit drop with season or weather, or among different plants. Most of the fall occurs during the spring and summer seasons, which are probably conducive to decay of the pedicels, and the least drop occurs during the winter. Heavy snows which bore the plants to the ground on several occasions produced no effect on fruit retention. On October 10, 1949, winds up to 89 mph as recorded 1.5 miles distant resulted in only a slight increase in fruit drop. Wind is probably of very minor importance in dispersal, since almost no fruits are shed during winter when they might be blown for some distance across a firm crust of snow. The fairly rapid drop-off of the 1949 crop before October is primarily due to the death or falling of

immature fruits which never developed beyond a very early stage.

Since wolfberry often occurs on flats or banks bordering streams, water may be of some significance in fruit dispersal, particularly during flood periods. A brief test showed that dry fruits will float in water for 48 hours before even half of them have sunk to the bottom of the container, although nine-tenths of the fresh fruits sink within this period. It seems that dry fruits could be dispersed for some distance by floods and occasionally be left on high enough ground to colonize.

DORMANCY

The type of dormancy present in the nutlets of *S. albus* (L) Blake (= *S. racemosus*) has been investigated by Flemion (1934, 1942) and Pfeiffer (1934), and that of *S. orbiculatus* by Flemion & Parker (1942). Both of these species have a double dormancy, requiring for germination both the breakdown of the mechanically restricting endocarp and impermeable integuments, and the after-ripening and development of the minute embryo. The breakdown of the coats is accomplished naturally by fungi in moist and warm soil, but can be hastened artificially by treatment with concentrated H_2SO_4. After-ripening and development of the embryo occurs during the colder seasons in soil in nature but may be accomplished artificially in a moist medium in the refrigerator for six or more months.

Very little work has been done on dormancy of *S. occidentalis* nutlets (U. S. Forest Service 1948). Experiments by the writer show that this species has the same general type of dormancy as *S. albus*. Without acid treatment the nutlets must remain in soil for two or more months, depending upon the activity of fungi in breaking down the coats, followed by several months of moist cold storage. Nutlets enclosed by fresh pulp are protected from coat decay for at least one or two weeks in warm and moist soil. No after-ripening occurs unless the coats are broken down prior to being given proper after-ripening conditions. Furthermore, fresh but mature nutlets which have not been allowed to dry do not after-ripen without pretreatment of the coats, apparently unlike the situation in *S. orbiculatus* as reported by the U. S. Forest Service (1948, pg. 35). Concentrated sulfuric acid treatment of dry mature nutlets for from 40 to 60 minutes at 30° C to 35° C was found to be a partial substitute for fungal action. As in the case of *S. albus* a short period of several weeks in warm moist soil following the acid treatment and preceding the cold temperature storage can considerably enhance the effects of the treatment. Attempts to substitute clipping or notching of the coats for the acid or fungal treatment were also made, but most of the nutlets so treated decayed during the subsequent moist-cold storage period. Passage through a bird or mammal digestive tract would probably speed the coat disintegration phase in those nutlets which were voided intact.

The length of the cold treatment necessary for after-ripening appears to vary considerably even among the nutlets of a single year collected from one colony. A range of 2.5 to 4.5 months at 5° C to 8° C in moist sphagnum or soil was the minimum time required for after-ripening of 1948 and 1949 crops. In one experiment appreciable after-ripening was obtained under almost constantly frozen conditions, at approximately –5° C. Both laboratory and field studies suggest that many of the nutlets probably require more than one summer and winter in the soil to break their dormancy, although moderate germination was obtained after only a single summer and winter, or the equivalent in the greenhouse and refrigerator.

Extraction of nutlets from dried fruits is readily accomplished by crushing the fruits after a few days of soaking in water, followed by flotation. Filled nutlets sink while empty ones remain on the surface with the greater portion of the pulp. Symphoricarpos nutlets are difficult to handle following after-ripening. During the after-ripening process the embryo elongates and it then not only occupies the entire length of the nutlet, but expands, with the still surrounding endosperm, so that the placental end frequently projects considerably beyond the coats. This may occur some weeks before after-ripening is even completed (Fig. 8B). An additional characteristic making it difficult to handle nutlets is that they germinate readily at temperatures just above freezing in moist media as soon as after-ripening has occurred. Furthermore, the embryos vary considerably in their after-ripening requirements. It was found that large quantities of after-ripened or nearly after-ripened nutlets could be kept more or less indefinitely by freezing the entire container holding the nutlets mixed with peat or soil soon after the first ones start to germinate. Recognition of this stage is facilitated by using a transparent container such as a beaker. Similar difficulties were experienced by Flemion & Parker (1942) in their study of *S. orbiculatus*. Their recommendations for obtaining seedlings in practical quantities by planting the nutlets directly in soil in flats and leaving outdoors during one summer and the following winter apply to *S. occidentalis* as well. This method is conducive to obtaining the highest germination percentages, up to 80% germination of initially filled nutlets having been obtained for wolfberry.

NATURAL STORAGE

Under natural conditions the fruits are subject to a great variety of environments after their maturity but before germination. This variety is increased because of the tendency of the fruits to remain on the shrubs for a year or more. Germination tests of fruits which had remained on the shrubs for up to four years show that the nutlets remain very dormant under such conditions. Since after-ripening will only occur following coat breakdown, the length of time the nutlet remains in the soil before germination is strongly affected by the season of the year it

is dispersed. Thus if the nutlet falls to the soil in the autumn the evidence suggests that in Minnesota coat breakdown by fungi will be insufficient to allow after-ripening and development of the embryo during the succeeding winter. Such a nutlet would probably require at least two winters in the soil to permit germination. On the other hand, many of those falling during the spring and summer, as the majority do, would require only one winter in the soil since the coats would have been thoroughly decomposed during the summer and fall.

A study designed to observe the progress of after-ripening under more or less natural storage conditions in the field was initiated in May 1949 with nutlets of the 1947 and 1948 crops. Sound nutlets were mixed with top soil from a Symphoricarpos colony and sewed in small bags made of glass cloth. The bags were placed in groups of four in a wolf-berry colony near Minneapolis. One half of the bags were buried just underneath the surface litter and the remainder were placed 4 cm deep and covered with sod. Bags containing a total of 500 nutlets were dug on approximately alternate months through August of 1950, except when they were frozen in the soil, and the condition and germinability of the nutlets observed.

Two months in the soil, especially at the 4 cm depth, broke down the coats sufficiently so that they could be readily split with a fingernail. By November 9 the embryos of the 1948 nutlets had elongated sufficiently to extend beyond the coats in 8% of those at 4 cm and in 4% of those at the surface. A last collection made on November 27 just before the soil froze showed 28% of the 1948 nutlets possessed a much elongated embryo from the 4 cm depth and 8% from the surface. A smaller proportion of the 1947 nutlets were elongated by this date at both depths. As was expected, germination tests yielded negative results from all collections made in 1949. Pairs of maximum—minimum thermometers at the two soil levels showed that temperatures during spring and summer were highly conducive to decomposition of the nutlet coats but not to after-ripening. Both levels were still fairly warm in October, and not until November did temperatures conducive to after-ripening occur, both depths then averaging close to 5° C. This probably explains the rapid increase in nutlets with greatly elongated embryos from November 8 to 27.

The first samples obtained in 1950 were those of April 15, and showed that after-ripening had been completed in at least a fair proportion of the nutlets. The surface storage yielded a lower germination percentage than did the 4 cm level, the germination of the 1948 nutlets being 31.2% for surface samples and 17.6% at the lower depth. Germination of the 1947 nutlets was approximately two-thirds that of the 1948 crop at both levels. Further tests on May 30, 1950, and again on August 10 and October 1 yielded no germination whatever of those nutlets which had not already germinated during early spring. Many of the remaining ungerminated nut-

lets, which by this time had been stored in the soil for two growing seasons and one winter, were alive but still quite dormant. The contents of some nutlets were decayed, more so at the surface than at 4 cm. It is highly probable that some of the viable nutlets would have germinated the following spring (1951), two warm seasons and two winters after having been placed in the soil, and possibly some of the nutlets may require an even longer period of soil storage than two years.

Investigations of nutlets stored naturally in the soil were carried out with the objective of discovering any which would germinate when given favorable conditions and of estimating their quantity in the soil. Samples of the surface 2 cm of soil 30 cm square were collected from the centers of ten heavily fruiting clumps near Minneapolis. The nutlets were recovered by washing the finer particles through a screen (20 meshes to the inch) and then individually selecting both empty and filled nutlets from the remaining debris. Only two seedlings were grown from over 4,000 nutlets thus recovered, and these only in very early spring. An average of over 200 nutlets occurred in each 30 cm square sample, but of these nutlets approximately 74% were empty, 25% had been chewed by mice, and only about 1% were viable as determined by embryo excision tests. Although the fairly large number of nutlets which occur in the soil are probably the accumulation of several years' crops, the proportion of after-ripened or even viable nutlets appears exceedingly small. This would suggest that extended periods of soil storage of viable Symphoricarpos nutlets are uncommon in nature.

The primary biotic agents destroying fruits and nutlets, once these have been dispersed and lie on or in the soil, appear to be mice and decay organisms. Two species of mice (*Microtus pennsylvanicus* Rhoads and *Peromyscus maniculatus* Bangs) were caught in traps baited with dry wolfberry fruits. As mentioned above, one-quarter of the nutlets recovered from soil samples in the Minneapolis area were evidently chewed and gnawed open by mice. Similar evidence of mice-feeding was obtained from soil-recovered nutlets at over half the remaining stations examined in the state. On the other hand, studies in which dry and fresh Symphoricarpos fruits were placed on the ground and individually marked with small stakes in several adjacent habitats near Minneapolis showed that only occasionally were the fruits disturbed. The marked fruits were observed at weekly intervals for a year, except when they were covered by snow. Mice again appeared to be the animal mainly responsible for those fruits which were utilized. At least one species of mouse climbs the stems and cuts off the fruiting branches which fall to the ground and are there used. The other major source of injury to fruits and nutlets after dispersal is decay organisms. Although a fair proportion of nutlets were observed to remain viable and unharmed after even two warm seasons in moist

soil, a number decayed during the first season although they appeared initially viable.

Seedling Stage

GERMINATION

Stages in the normal germination of *S. occidentalis* are illustrated in Fig. 8. Usually some time before germination proper begins the embryo and surrounding endosperm expand to the full length of the nutlet and somewhat beyond (Fig. 8B). Germination commences with the breaking out of the radicle at the end of the nutlet where the endosperm is exposed (Fig. 8C), and is epigeous. The hypocotyl expands and pulls the now rapidly developing cotyledons upward through the soil, after the elongation of the radicle to a cm or more (Fig. 8D). By the time the cotyledons are expanded the primary root may be two to four cm long (Fig. 8E). The coats are often shed while they are still underneath the soil surface, but occasionally they stick to both cotyledons in which case the seedlings are abnormal or "coatbound."
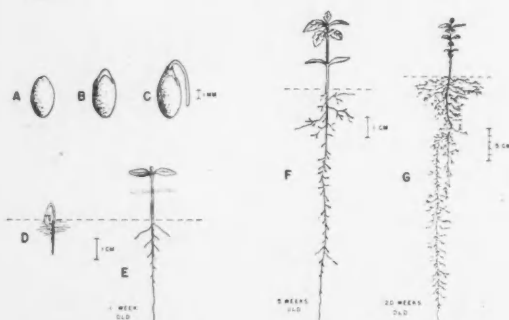
Fig. 8. Germination and seedling stages of plants grown out-of-doors in fine loamy sand during 1950.

The observation that fully after-ripened nutlets will not germinate readily at room temperature or in the field during summer, and yet will do so while under refrigeration or as soon as the soil thaws in the spring, initiated an investigation of temperature effects. Two-hundred mostly after-ripened nutlets were kept in moist chambers under each of the temperature conditions given in Table 3. The results show that low temperatures definitely favor germination, while even temperatures of 20° C strongly inhibit it. Of the constant temperatures 10° C appears to be the most favorable, alternating temperatures of 5° and 10°, 5° and 15°, and 10° and 15° giving similar results.

It was also observed that many nutlets will germinate in relatively poorly aerated containers in the refrigerator. A comparison was made of germination in moist covered Petri dishes, in frequently changed water in open Petri dishes, and in unchanged water in closed Petri dishes. Surprisingly, the non-aerated water-filled dishes gave the highest germination (76.3%). The aerated water medium yielded 71.2%, while the most chamber only 59.2%. Since wolfberry nutlets usually germinate in early spring when the soil is cold and saturated, poorly aerated germination media are probably normal for the species in nature.

Although no laboratory studies of the pH tolerences were made, a comparison of germination and seedling development on sandy soils of pH 5.9 and 7.3 showed no appreciable differences between the two pH levels.

ESTABLISHMENT

Establishment may be strictly defined as having occurred when the seedling plant has utilized the food reserves of the seed and is dependent upon its own photosynthate. At least by the time the cotyledons of *Symphoricarpos* have expanded the remains of the endosperm have been absorbed. Hence the period of establishment in this group is of very short duration. The cotyledons are green and photosynthetic and may not be followed by the first pair of true leaves for several days. During the brief but critical period of germination and establishment, numerous injurious factors may take a significant toll. About 1 to 2% of the seedlings observed in 1950 were coat-bound. Birds, snails, and insects frequently clipped off the cotyledons or chewed the hypocotyl, and damping-off fungi attacked many seedlings even before they were above the ground. Emerging seedlings of *S. occidentalis* probably escape a large proportion of invertebrate animal feeders and competition from other plants by germinating as soon as the soil has thawed in very early spring. A transitory dry spell in early spring was observed to be disastrous to *Symphoricarpos* seedlings which had just completed or were in the process of germination, even though the soil was wet just below the surface. Yet as described below, a much greater mortality was observed following germination and establishment than occurred during this brief period.

Table 3. Germination of after-ripened nutlets under different temperature conditions, each percentage based on 400 nutlets. Final count taken at two weeks. The nutlets under alternate conditions were exposed to the high temperature for 8 out of each 24 hours.

| | Constant Temperatures (°C) | | | | | Alternating Temperatures (°C) | | | | | | | | | |
	5	10	15	20	25	−5 & 5	−5 & 10	5 & 10	5 & 15	5 & 20	10 & 15	10 & 20	10 & 25	15 & 20	15 & 25
Percent germination......	35.5	44.1	40.1	18.7	5.9	0	0	45.2	45.7	35.3	45.8	37.0	29.4	22.3	20.1

JUVENILE STAGE

SEEDLING DEVELOPMENT

The first pair of true leaves are quite similar in appearance to the leaves of the mature plant except for their smaller size. Root development is rapid at this stage. Figure 8 shows seedling characteristics and the relative development of root and shoot of plants grown out-of-doors during 1950 in a fine sand collected from a Symphoricarpos colony. In the relatively infertile soil the plants developed poorly, their shoots reaching only 9 cm in height by the end of the first growing season (Fig. 8G). Another series of seedlings grown in rich potting loam made excellent shoot growth, reaching 45 cm in height by the same date. Their leaves were also up to five times the size and much darker green than those grown in the sand. A comparison between seedlings of these two groups is illustrated in Fig. 9. Although wolfberry frequently grows in relatively infertile sands it appears that seedlings are notably responsive to fertile soils. Even the vigorous seedlings produced neither rhizomes nor flowers during their first year, however, and time limitations prevented study of later stages of growth.

FIG. 9. Two five-month-old seedlings grown outdoors during 1950. The large plant was grown in rich potting loam, and the small one is in loamy sand which was collected from near the center of a Symphoricarpos colony. The small plant approximates the average size of naturally-grown plants observed in the field during 1950, and is similar to that illustrated in Fig. 8G.

Excavations indicated that roots of the seedlings grown in the fine sand penetrated rapidly for two to three months after germination until they became strongly mycorrhizal in appearance, after which depth penetration appeared to slow or cease completely. A pathological condition may be involved other than simply strongly developed mycotrophy, for the entire root system of many other seedlings grown in the same soil was so injured that the shoot was very stunted and frequently died. Root aphids

(Aphididae) were also injurious to a few of the seedlings grown in both sand and loam. Root systems of field grown seedlings are described below.

A study of some of the factors which appear to be most destructive to the plants during their first growing season was undertaken on May 19, 1949. Quadruplicate 30 cm square seed plots were planted in each of the closely adjacent habitats near Minneapolis which are named in Figs. 11 & 12. The plots were of such a size that they might easily be comparable to numerous regularly occurring natural disturbances such as, for example, an abandoned gopher mound. It is probable that wolfberry seedlings rarely become established naturally except in these or similar situations, as has been suggested by Bird (1930) and Moss (1932), and by observations of naturally occuring seedlings described below. Three depths of planting were used in each plot, 2 mm, 6 mm, and 12 mm, and all plots were covered with a thick mulch which was not removed until April of 1950. The soils were quite similar in all habitats, the pH ranging from 6.0 to 6.6 and texture showing only minor variations, all the soils being sandy loams. Soil moisture averaged consistently 2 to 3% higher in the elm (Ulmus spp)–ash (Fraxinus spp) forest, while that in the bur oak (Quercus macrocarpa)–wolfberry community averaged slightly lower, in comparison with the remaining situations. Light conditions were varied; at ground level it was only 5% of full sun in the elm-ash forest, 15% under bur oak-wolfberry, 25% under the dense wolfberry colony, 75 percent under the sumac (Rhus glabra) canopy, and 100 percent in the open grass (Poa pratensis). Climatically, the growing season of 1950 was not abnormal for the locality, and rainfall (Fig. 10) and temperature conditions appeared to be much more favorable for seedling survival than during the previous year.

The nutlets germinated and were marked with toothpicks as soon as the soil thawed in mid-April of 1950, but some germination continued into May. By far the best stand resulted from the 12 mm depth of planting. Four major types of injury to seedlings were recognized. A large number were found clipped
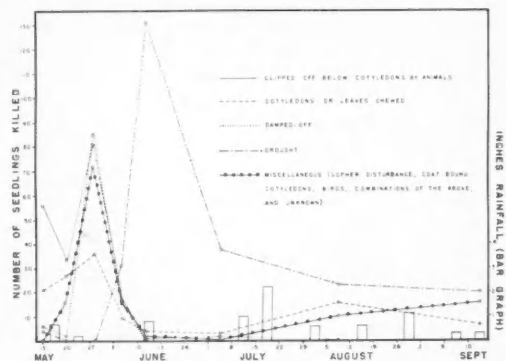
FIG. 10. Seasonal variations in causes of seedling death on all field plots during 1950, together with precipitation records.

off somewhere between ground level and the cotyledons. Tests using small cages showed that the agent responsible must be able to pass through a 3 mm mesh screen or, more likely, resides in the soil within the cage. Two species of small snails and a slug were observed on the plots, but perhaps other invertebrates are more important in this regard. Another major type of injury was that in which the cotyledons or leaves were so seriously chewed as to result in death. Since there were all gradations between this type of injury and the preceding, and as the cage had no influence here either, probably the same agents were partially responsible for both. Damping-off fungi and drought injury were the two other major causes of mortality. In the miscellaneous category is included those numerous cases where death could not be attributed definitely to one of the preceding causes, or where the seedlings had disappeared. Here also are the fairly large number which were destroyed by gopher activity on a relatively few of the plots, the seedlings which died from the coat-bound condition, and the very few seedlings which were found pulled out of the ground and left on the surface, perhaps by birds.

Figure 10 shows the seasonal variations in causes of seedling mortality on all plots during their first year. The drought of late May and early June was the single greatest cause of death since the seedlings were still very undeveloped. Somewhat sooner after germination destructive biotic agents predominated, including both animals and damping-off fungi. A comparison of mortality in the different communities is illustrated in Fig. 11 which shows that the plants in the elm-ash forest had an appreciably lower mortality rate than did the others. It is doubtful that the seedlings would survive for more than one more year in the forest, however, as a result of the relatively dense shade. In general, mortality was comparatively slight during the germination period, increasing rapidly to a maximum, and finally leveling off as few survivors were left. Figure 12 illustrates the fact that different causes of mortality predominated in different habitats.
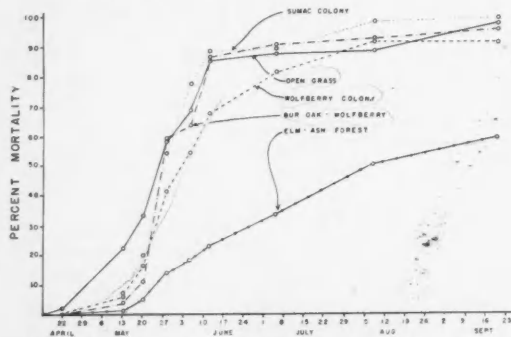
FIG. 11. Comparison of seedling mortality on seed plots in five adjacent communities during 1950. One hundred percent on the ordinate represents the total initial number of seedlings on all plots within a given community, ranging from 102 to 275 for each habitat listed.
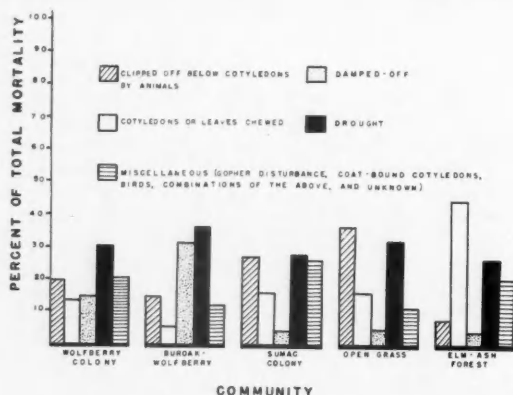
FIG. 12. Causes of seedling death in each of the five communities by the end of the first growing season.

The growth of the seedlings was not vigorous on any of the plots. Looking very similar to the small plant in Fig. 9, no seedling exceeded 10 cm in height. The root systems of seedlings growing in the open grass plots reached a maximum of 35 cm by the end of the season, while those of seedlings grown in the dense shade of the elm-ash forest attained only one-fourth this length. The shoots were of approximately equal height in the two extreme habitats, however, thus resulting in very different shoot-root ratios and greater potential susceptibility to drought in the forest-grown plants.

Careful search throughout 1949 failed to demonstrate a single seedling in or adjacent to colonies. More success was attained in the more favorable season of 1950, although in a late June survey of the state, seedlings were found at only three out of twenty localities examined. Seedlings were never found in the dense bluegrass sod which is normally present in and around colonies of wolfberry in Minnesota. Two were found next to a badger hole within a colony but the rest occurred near the centers of dense clumps where the sod had been shaded out and where the young plants would never be expected to survive. Of 50 such seedlings staked on May 30 near Minneapolis, 20 survived through July 5 and 7 through September 20. The causes of death were essentially the same as those described above for the seed plots (Fig. 10), and drought appeared again to be the major factor. These natural-grown seedlings were likewise very weak, none exceeding 6 cm in height.

SUCKER DEVELOPMENT

Sucker shoots originating from rhizomes are far more common in nature than are seedlings of *S. occidentalis*. The rhizome suckers develop in spring at approximately the same time the shoots are developing on the older stems. In their first year they frequently attain almost the full height of the mature stems, and sometimes even fruit abundantly. The sucker shoots usually are reproductively mature for a number of years before the rhizome connections

with the parent stem are severed or decay. They are probably essentially independent of the parental shoot by the end of the first growing season, however, since the sucker and attached rhizome segment develop their own root system.

REPRODUCTIVE STAGE

SHOOT CHARACTERISTICS

Near Stations 5 and 10 colonies range up to an acre or more in extent (Fig. 1), but elsewhere they were observed to be much smaller, largely owing to restriction by cultivation, roads, forests, and topographic features. Sometimes, in fact, there are few distinct colonies over a half meter in diameter, as at Stations 13 and 16, probably owing to weakening of the clumps by heavy shading combined with browsing and trampling. Usually, however, colonies range in size from a meter or two to 50 or 75 meters in average diameter, frequently extending as a narrow strip for long distances along streams or along the edge of a forest border (Fig. 2).

Stem density within a colony varies considerably, but in most localities there are colonies of low average density and also those of high average density (Fig. 3). At only half of the stations examined were there any colonies dense enough to completely shade out bluegrass at their densest portion. The densest as well as the tallest colonies are most commonly located on the sites which are both relatively moist and exposed to full sun.

The average colony height for all stations examined was estimated at 75 cm, but ranged from about 40 to 110 cm at different localities for mature fruiting stems. The maximum heights of stems at the 20 stations varied from 70 to 170 cm, averaging 115 ± 5.5 cm. Stem height showed no obvious correlation with any other environmental factor than soil moisture, clumps on southerly exposures being considerably lower than those on north-facing slopes or on stream flats. Mean maximum stem diameter at 3 cm from the ground averaged $1.27 \pm .07$ cm for all stations, the maximum ranging from 0.83 to 2.00 cm. The stems are quite flexible, and a full crop of fruits and foliage, coupled with the effects of snow and ice, tends to partly bend over many initially erect shoots which then retain this habit.

The leaves also present considerable variation in different habitats. In dry unshaded situations on infertile or shallow soil they are yellowish green, entire, small, and tend to be somewhat vertically oriented, while they were observed to be usually dark green, large, somewhat lobed, and horizontally oriented in moist, fertile, and partly shaded habitats. These differences may be noticeable between leaves occurring on stems growing in full sun and on stems of the same colony which extends under an adjacent forest canopy, such instances eliminating the genetic factor since a single clone is involved.

Some of the above observations also have been recorded for other regions in a number of the local studies mentioned under Distribution above. In addition, quantitative quadrat studies were performed by the writer on several colonies near Minneapolis. It was found that one of the most conspicuous relations is the trend toward greater stem height as the center of the colony is approached. Stem diameter demonstrates the same general trend as height, as was expected from the moderate degree of correlation suggested by scatter diagrams of these two characteristics. Although stem density was usually much the lowest near the periphery, in half of the clumps the intermediate section was denser than the center (up to more than 50 stems per sq. m.). No distinct colony which was examined anywhere in the state possessed a "hollow" center. The mean and maximum stem ages tend to increase toward the center of the clump. Different types of age distribution are illustrated by two colonies in Fig. 13. The major differences between the two is explained by a fire which burned Colony C but missed Colony F five years previous. Determination of rhizome ages shows that both colonies are actually older than twenty years.
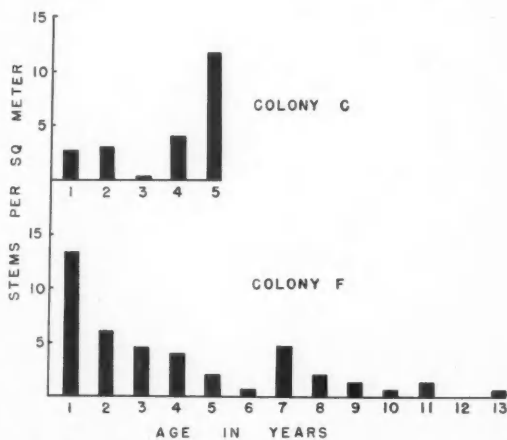
FIG. 13. Two types of age distribution of stems from two colonies at Station 4. Colony C had been burned five years before but Colony F escaped the fire.

In Minnesota wolfberry appears to leaf out as early as any of its associated woody plants, and considerably earlier than some. Furthermore, its leaves are quite persistent in the fall, remaining at least yellowish green later than many of its woody associates, and a few leaves remain in a brown and dried condition on the shrubs all winter. The shoot buds began swelling in 1950 by the abnormally late date of April 20 in warm locations near Minneapolis. The official mean temperature for the week of the beginning of bud expansion was 45.3° F, as contrasted with the two preceding weekly means of 33.1° F and 29.4° F, which had been the warmest of the season. In the absence of injury there is normally but one cycle of shoot growth per year in Minnesota, that in the spring, which ends with the initiation of flower

buds at the apical nodes. If later cycles of flower
buds are produced, a few new leaves may precede
their formation. Tests described in a subsequent sec-
tion indicate that day lengths longer than at least
14 hours can strongly stimulate vegetative growth.
The winter buds of *S. occidentalis* do not appear to
require very prolonged chilling in order to open
normally in the spring. Buds on stems collected
December 10, 1949, and placed in water in the green-
house did not grow, but stems brought in on Decem-
ber 20 developed shoots one inch long within two
weeks. These latter stems had been exposed to mean
temperatures of 48° F or below for 55 days before
being collected. The chilling requirement of *S. occi-
dentalis* probably nowhere limits its natural distribu-
tion, since everywhere around the warmer borders of
its range the winter cold greatly exceeds this mini-
mum requirement found for a Minnesota clone.

ROOT DEVELOPMENT

No references to previous excavations of *S. occi-
dentalis* roots have been discovered by the writer,
although those of *S. orbiculatus* have been investi-
gated. In the present study the root system of wolf-
berry was exposed in a uniform and deep fine loamy
sand near Minneapolis, following Weaver's (1919)
methods. A four year old fruiting stem of moderate
vigor was selected near the edge of a colony in a
dense bluegrass sod. The root system of an attached
80 cm section of rhizome of the same age as the stem
was excavated and mapped to scale (Fig. 14). A
characteristic of the roots originating from the rhi-
zomes is their tendency to arise in pairs at the rhi-
zome nodes, one root just below each paired bud, but
subsequent unequal growth obscures this relationship
and only a few roots penetrate deeply. The roots
become increasingly mycorrhizal in appearance as the
tips are approached, the latter becoming yellowish
or whitish, stubby and thickened, with a fine cover-
ing of closely adherent soil particles. The greatest
depth to which the roots penetrated was 155 cm,
although the soil was uniform and drained to a
greater depth than this. The root system examined
was a young one, however, not exceeding four years
old.

RESISTANCE TO EXTREMES

In general, mature wolfberry clumps appear highly
resistant to many physical and biotic extremes.
Among the greatest of the physical extremes to which
the plants are subjected is winter cold. At almost all
the localities studied in 1950 slight to severe dieback
even down to ground level occurred in at least a few
scattered stems in each colony, this being especially
prevalent at Stations 12 and 18. The stems were
dead one-third to three-fourths from the tip and had
resprouted from lower buds. Since no evidence of
other destructive factors was obtained it is quite pos-
sible that winter killing may be involved.

Although exposure to full sun is the most common
situation for wolfberry in Minnesota it occasionally
penetrates forests intercepting all but about 5% of
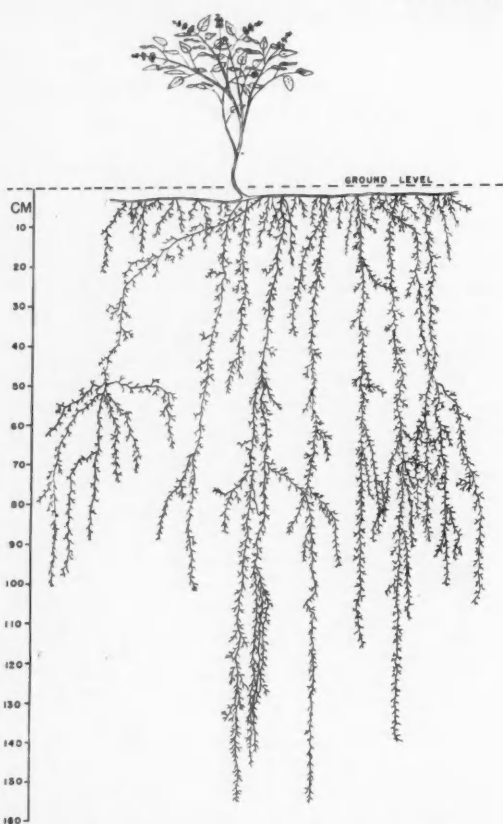
FIG. 14. Profile view of the root system of wolfberry
arising from a four-year-old rhizome in a uniform and
deep fine loamy sand.

the sunlight reaching adjacent open areas. It is not
likely that the shrub is naturally tolerant to shade,
for it probably penetrates shaded habitats only by
rhizomes, or else overtopping vegetation develops
after the colonies are already established. The latter
is apparently occurring in the pine forest at Station
16, mentioned above.

Snow and glaze ice will bear the flexible stems to
the ground, but breakage was never observed. The
stems are so low and flexible that even winds of
near hurricane velocity do not produce any noticeable
effect on the colonies. In slight depressions water
may accumulate during an early spring thaw. Al-
though the partly to completely submerged stems may
be subsequently frozen in solid ice several times no
harm appears to result. Well established colonies are
probably highly resistant to drought. In a transplant
experiment on prairie and plains in Nebraska using
rhizomes of *S. occidentalis*, Clements & Weaver (1924)
found that wolfberry survived longer than most of
the other species of trees and shrubs used in the ex-
periment, including *S. orbiculatus*. Other soil and

climatic conditions which the species appears to tolerate have been described above under Habitats.

Although the stems of wolfberry are sensitive to fire the rhizomes and stem bases appear unharmed, probably because of their depth in the soil (2 to 35 cm), and recovery is moderately rapid. A brief study was made of a partly burned colony of wolfberry near Minneapolis, comparative data being obtained from adjacent quadrats in burned and unburned portions. The fire spread through the dense bluegrass sod in mid-April before Symphoricarpos had begun to leaf out. Although the stem bases were only barely charred, all stems were killed to the ground. By fall of the same year in which the fire occurred the sucker shoots on the burned area averaged less than half the heights and diameters of the unburned stems, but an average of 2.5 young shoots sprouted from below the ground near the base of each killed stem. This effect of fire increasing the number of stems but decreasing their size was also found by Aldous (1934) with *S. orbiculatus*. Height growth during the second year was appreciable, most of the stronger stems reaching three-fourths of the height of those which were unburned. Stem density had by this time been reduced somewhat on the burned portion by competition but was still very high. At least in the more humid parts of its range, occasional fires may favor *S. occidentalis* by reducing competition from taller vegetation, but annual or very frequent fires are probably detrimental wherever the shrub occurs.

A number of injurious biotic agents also affect the shrub. Many insects attack the vegetative parts, but during 1949 and 1950 none of these appeared to be of major importance. Although a number of lepidopterous larvae were among the leaf chewers, only one even approached epiphytotic proportions in any single locality examined, this being a large hawk moth larva (Sphingidae) at Station 9. The leaves and shoots were injured by aphids (Aphididae) almost as much during 1950 as by chewers. Mealy bugs (Coccidae) were of minor importance. No fungus diseases of significance were observed on the vegetative parts during 1949 or 1950. A white crust-like mycelium of what is probably Corticium was found occasionally at the stem bases in dense colonies, but this was not observed to seriously injure the stems. A list of 42 genera and 50 species of fungi which have been found occurring on *S. occidentalis* is catalogued by Seymour (1929). Stem girdling by mice or other rodents was observed only at Station 9 and winter browsing of the stems by rabbits occurred at Station 4.

Wolfberry appears to be quite resistant to browsing by livestock in Minnesota, probably mainly because of its comparative unpalatability and active vegetative reproduction. Although damage to the colonies sometimes occurs through browsing and especially trampling, it seems that the weakening of the competitive sod by grazing more than compensates the shrubs for the damage done directly. This perhaps accounts for the general consensus of opinion which was confirmed by the writer that wolfberry often increases under overgrazing (Pound & Clements 1898; Clements 1920; Dr. E. W. Tisdale and Mr. A. H. Larson, communications). Observations by Dr. Tisdale in Canada indicate that *S. occidentalis* tends to spread on overused ranges and pastures in the moister parts of the western plains and in the aspen parkland zone, but in the drier areas its abundance seems less affected by grazing intensity.

Numerous attempts have been made to eradicate *S. occidentalis* from pastures, but the shrub appears resistant to all the common methods of eradication which have been attempted. Grubbing out the stems is generally ineffective because of the abundant rhizomes. Fire, if used at the period ow low food reserves, has been shown to be effective in a single season with *S. orbiculatus* (Aldous 1934). Cutting in spring for three successive years has also been successful with this latter species (Aldous 1935).

During 1949 exploratory cutting experiments were performed on *S. occidentalis* at monthly intervals on small numbers of individually marked stems in dry and moist habitats. No stem resprouted during the same season it was cut if this were not done before early August, apparently owing to normal bud dormancy and even most of those cut in June and July delayed resprouting until the following year. Lightly topped stems frequently died partly or all the way down to the ground, especially if they were cut after the shoot buds had become dormant in summer. The only kill of even partial effectiveness was obtained from an early August cutting on the drier site. Under moist conditions not only did all the stems survive, but a much larger percentage of them resprouted the same season they were cut. Severity or height of cutting seemed to have little or no effect on survival, only season and site influencing the results significantly.

Because of the difficulties of eradicating wolfberry by the methods mentioned above, resort is now being made in an ever increasing degree to the chemical herbicides. The most promising herbicide is 2, 4-D, and yet *S. occidentalis* is one of the more resistant shrubs to this chemical (North Central Weed Control Conference 1949). At least in Minnesota probably the most effective and economical way of preventing the establishment and spread of colonies by both seeds and rhizomes is conservative pasture use and the resulting maintenance of a dense competitive sod.

RHIZOME REPRODUCTION

The highly developed rhizomatous habit of *S. occidentalis* is largely the basis for both its aggressive weedy characteristics and its erosion-control, browse, and wildlife values. The shrub appears to have become dependent upon rhizomes for survival and local propagation. The species, however, seems to be dispersed over some distance only by seeds, and probably reproduces sexually with sufficient frequency to maintain its genetic diversity and consequent adaptability to changing conditions. Unlike certain other species of *Symphoricarpos*, *S. occidentalis* bears neither runners nor regularly layers.

A portion of a single interconnecting rhizome system from a relatively open colony growing on fine loamy sand near Minneapolis was excavated and is represented in Fig. 15. The rhizomes tend to be very long and sparsely branched. No conclusive evidence was found of decaying rhizome sections which would allow separation of an original clump into separate colonies, but the rhizome system illustrated was less than ten years in age. Although the lateral buds occur in pairs on the rhizomes the branches generally arise only one at most per node, and even these occur sparsely. The average diameter of the rhizomes of Fig. 15 was about 4 mm, but they are usually considerably larger near their junction with another rhizome branch or erect stem. In the colony represented by Fig. 15 there is a greater cumulative length of rhizomes than there is cumulative length of erect main stems, the ratio being 4.4 cm of rhizome to 1.0 cm of live aerial stem. Whitish and succulent rhizome growing tips were occasionally found, but natural grafts were observed in only one colony examined.

FIG. 15. Vertical view of a portion of a single interconnecting rhizome system of an open colony growing on loamy sand. o =live erect stem; ● =dead erect stem; =rhizome not traced further.

In order to gain some idea of the actual density of rhizomes produced per unit area of ground surface two plots one square meter in size were excavated (Fig. 16). The upper plot of the figure was located near the apparent center of the same open colony of which part is shown in Fig. 15, and the lower plot was diagrammed from an adjacent dense clump from which the sod was excluded by shade. The thick sod may have exerted an influence in keeping the rhizomes of the upper colony of Fig. 16 farther below the surface than those of the lower colony. Much deeper rhizomes were found elsewhere, down to a depth of 35 cm at Station 14 in the heaviest soil observed for the species, a clay loam. For any given rhizome the depth varies considerably, usually being greatest some distance from the aerial stems.

A study of several colonies near Minneapolis was made in order to determine the period of most rapid
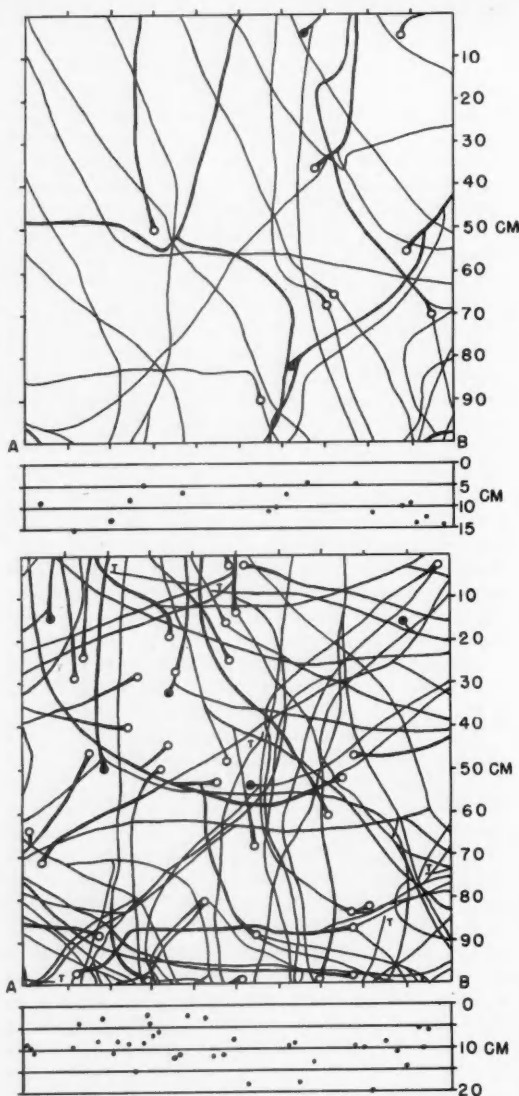
FIG. 16. Comparison of the entire rhizome system within one square meter of a moderately open colony above and a very dense colony below, both occurring on loamy sand. Rhizome depths are shown for the sections A-B. o = live erect stem; ● = dead erect stem. T = rhizome tip.

vegetative spread. Two perpendicular transects were laid out intersecting at the apparent center of the colony, and age counts were made on the oldest rhizomes to be found along each transect. By this method the earliest date on which a given unoccupied zone was invaded by the expanding clump was roughly estimated, as represented in Fig. 17 for one colony. It seems that the growth was not notably restricted to any particular period, but varies con-
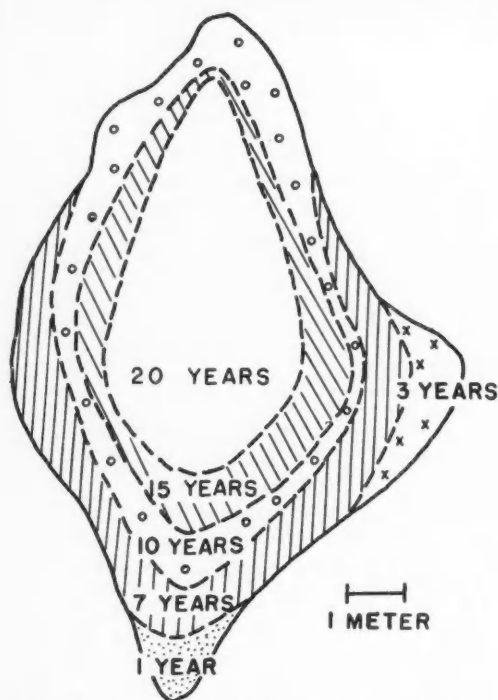
Fig. 17. Age zones indicating rate of spread of one colony at Station 4. Years refer to the oldest rhizomes found within a given zone.

siderably in different parts of the clump in different years.

The rhizomes appear to be resistant to a variety of extremes. Observations of plants growing under conditions of poor drainage are mentioned above. Rhizomes seem to be protected from fires by their depth in the soil, and no insects or fungi were observed to attack them. The considerable length of time that they may remain interconnected without sections dying, as mentioned above, testifies to their hardiness.

Vegetative propagation of wolfberry is said to be accomplished readily by hard or softwood cuttings of aerial stems or "roots" (=rhizomes?) (U. S. Forest Service 1936; Van Dersal 1938). Roots formed readily on both suckers and older stems brought into the greenhouse by the writer on December 20, 1949. Although the water in which they were placed was left unchanged and unaerated for over two months an abundance of roots was produced, suggesting a rather high tolerance for poorly aerated media. Stems treated similarly while in full leaf in August produced no roots at all, however.

FLOWER BUD DEVELOPMENT

The broad and pinkish flower buds are formed near the growing tip of a young shoot as the end of the spring flush of growth approaches. Each visible flower bud develops into a spicate cluster of about 5 to 20 buds, two to four of which usually open each day. In 1949 the first visible flower buds appeared on plants in the field about May 20, and new flower buds differentiated at successively lower nodes as the season advanced.

The observation that the flower buds of *S. occidentalis* differentiate during the period of long days from the middle of May through the middle of August suggested a possible photoperiodic response. This hypothesis was tested by transplanting 16 stems from a colony into pots, and subjecting groups of four stems to known daylengths by means of large light-proof aluminum boxes and supplementary 15 watt white fluorescent lamps. It was found possible by this means to manipulate the flowering behavior almost at will, since the plants which were tested responded strongly to long photoperiods. The day length of 14 hours appears to be close to the "critical" one, for photoperiods shorter than this inhibit all flower bud initiation, and prevent normal vegetative growth in addition. Once the flower buds have reached visible size their subsequent development is not dependent upon long days. Considering the wide latitudinal range of *S. occidentalis*, clinal variations in photoperiodic response are probably to be expected. Even if such genetic variations were absent photoperiod requirements probably nowhere limit the present range of the species, since sufficiently long days occur in summer far south of its present distributional limits to permit normal flowering.

The temperature requirements for flower bud formation do not seem to be exacting. Buds were produced outdoors in the summer of 1949 when the average maximum temperatures were 90° F and the average minimum 70° F, while they were also produced fairly abundantly in winter under long photoperiods in the greenhouse with an average maximum temperature of only 61° F and an average minimum of 51° F.

There is a moderate mortality of flower buds before they open, as a consequence of various injurious agents. Insects frequently consume young flower buds, but during 1949 and 1950 this was a minor cause of mortality. Much more important in this regard, especially in the very warm season of 1949, was a disease which caused the unopened corollas to turn brown and decay just as the bud approached anthesis. *Alternaria* sp. may be the causative agent.

ANTHESIS AND POLLINATION

Most references to phenology of *S. occidentalis* give the flowering period as "June–July," but Fernald (1950) states it can occur from "Late May to September." In 1949 anthesis of the earliest flowers in the vicinity of Minneapolis began on June 12, and although a few of the clumps continued flowering until September 14, most had ceased by August 15. Flowering tended to occur in two or more cycles during the warm summer of 1949, but enough overlap occurred so that many plants were in continuous bloom for much of the summer. Anthesis does not

require long days and occurs under the same range of temperatures given above for flower buds.

The flowers open during the night or early morning. The very sticky pollen grains are comparatively large, expanded grains in lactic acid showing a range of 51.1-60.1 μ. Rough counts of pollen production indicate that this may vary from 600 to 800 grains per anther. Counts of empty or shriveled grains showed less than 0.2% of the total number examined were obviously defective, but results from pollen germination tests were erratic and inconclusive. The corolla, together with the five attached stamens, is often shed while some pollen still adheres, for the tube seldom is retained on the inferior ovary longer than three or four days.

The slightly fragrant flowers are insect pollinated. When open, the corolla is wider (10-12 mm) than it is deep (6-9 mm). The wide-mouthed corolla tube is only 3-4 mm long, the lower 2 mm of which is filled with nectar. The nectar is generally concealed from view by abundant water-repellent hairs. Not all the flowers are protected from rain by a pendulous position since they face outward from the dense clusters in all directions.

No special mechanisms which tend to favor cross-pollination or limit self-pollination appear to be present, other than the tendency for self-incompatibility discussed below. The stigma and anthers are slightly to moderately exserted, on essentially the same level, and appear to mature simultaneously. Autogamy is probably very rare. The pollen is not shed until the flower is fully open and tends to adhere firmly to the dehisced anthers if untouched. The anthers spread widely outward from the style and do not undergo growth or withering movements which might bring them into contact with the stigma.

The relatively simple and accessible structure of the flower would suggest that it is not specialized in such a fashion as to favor only certain species or types of pollinating animals. The following pollinators were especially abundant on flowers in 1949 and 1950 near Minneapolis: HYMENOPTERA—*Bombus* spp, *Apis mellifera* L., *Eumenes* sp., *Chlorion pennsylvanicum* L., and *Palistes* sp; LEPIDOPTERA—*Basilarchia archippus* Cram., *Vanessa atalanta* L., *Epargyreus tityrus* Fabr., and *Minois alope* Fabr. Somewhat more than half the HYMENOPTERA were long-tongued, the remaining being short-tongued types. Honey bees, bumble bees, wasps, and hornets among the HYMENOPTERA visited the flowers with about equal frequency. The LEPIDOPTERA combined seemed to be of only slightly less importance in terms of frequency of visits than any one of these hymenopterous groups. This wide range of pollinator types probably tends to insure good pollination in even the most unfavorable seasons, particularly since the flowering period is normally quite long.

Emasculation and bagging tests failed to show any parthenocarpy or apomixis. Although East (1940) states that all species of Symphoricarpos are self-fertile, some experimental results obtained by the writer indicate that this may not be unqualifiably true. Nearly mature but unopened flower buds were enclosed with paper bags on stems of one colony near Minneapolis. For selfing, pollen from the same flower or from flowers in the same bagged inflorescence was applied with a sterile tweezers to naturally opened flowers for two successive days, each time followed by rebagging. The procedure for crossing was similar except that fresh and one-day old pollen was collected from a colony several miles distant and applied similarly for two successive days. The bags for both selfing and crossing were kept on until the corolla tubes and styles had abscissed. Over a period of six weeks 59 flowers were selfed and 50 were cross-pollinated. Under the conditions of the experiment only a relatively small percentage (15.2%) of fruits set and matured from their own pollen while a high percentage (84.2%) set fruit from crossing. Cutting tests of the mature seeds produced by both selfing and crossing showed no visible difference, the embryos being normal-appearing in both.

Although a rather large variety of insects may feed occasionally upon flowers and pollen, very little unfruitfulness was observed which could be attributed to such injury during the seasons of 1949 and 1950. Certain insects sometimes eat holes through the base of the corolla tube, presumably thereby obtaining the nectar without effecting pollination, and pollen eating beetles may be common. Frequently the petals and other flower parts are eaten by chewing insects. No significant injury to flowers was observed to result from unfavorable climatic conditions during the investigation.

FRUIT AND SEED DEVELOPMENT

Abscission of the corolla tube is succeeded by the gradual enlarging of the ovary for a period of several weeks, during which time the color of the fruit gradually fades to a pale greenish or yellowish white. A considerable variation in the size of the nutlets occurs even among fruits from a single plant. Most commonly two normal-appearing nutlets are present in each mature fruit, but occasionally a fruit has one full sized nutlet and one flattened nutlet, and rarely a fruit with three sound-appearing nutlets is found. Filled nutlets with a moisture content of 8.2% weigh an average of 0.00653 grams each, which is slightly heavier than the figure given by Stevens (1932).

Fruit maturation does not have definite photoperiodic requirements, and the temperatures necessary for adequate ripening are at least as broad as those required for bud development mentioned above. Jones (1940) has observed that wolfberry plants are frequently sterile in dry shaded habitats. The species can produce at least some fruits in fairly dense shade in Minnesota, however, and fruiting is sometimes little or not at all affected by moderate shade (25% of full sun).

Quantitative studies of several colonies near Minneapolis were performed in 1949 with the objective of noting any correlations of fruit produc-

tion with the height, diameter, and age of stems, or position of the stem in the colony. The greatest number of fruits borne per square meter was over 3,000, and that borne by any single stem was 550. Although no heavier producing stems were observed anywhere in the state this latter figure is only equal to what Stevens (1932) has estimated is the "average" production in North Dakota. Fruit production tends to increase markedly from the periphery toward the center of the colony. With certain exceptions the percentage of the total stems which bear fruits also increases towards the center, and the same tendency is present in the mean number of fruits per stem. The poorer fruiting of the stems near the periphery appears to be caused by the younger average age of the stems and also by the more severe competition with the grass sod in this location.

Table 4 shows the progressive changes in mean fruit production with increasing height, diameter, and age of the stem. Strong tendencies for fruit production to increase with both increasing stem height and diameter are shown. This trend appears much weaker for any single colony in the case of age, but the overall average of all colonies does present a positive relationship. Using a single age class a positive correlation was also shown to exist between two measures of vegetative vigor of stems, height-age ratio and diameter-age ratio. That is, greater vegetative vigor, as measured by growth in height or diameter per unit of time, is correlated with greater average fruit production among stems of a given age.

Counts of fruits set and matured, expressed as a percentage of the total number of flower buds produced, were made on six stems near Minneapolis. Of a total of 962 buds produced on these six stems, an average of $74.6\pm7.6\%$ matured fruits, the range be-

TABLE 4. Relation of fruit production per stem to stem height, diameter, and age for six colonies of S. occidentalis.

Measurement	Size or age class	Total No. of stems	Mean Number of Fruits Per Stem						Mean for size or age class
			Colony						
			A	B	C	D	E	F	
HEIGHT	0-24 cm	7	....	....	0	0	....	0	0
	25-49	58	0	0	0	0	0	0	0
	50-74	110	0.8	0	0	29.3	2.2	0.8	5.5
	75-99	117	5.9	4.2	30.6	33.9	19.7	18.5	18.8
	100-124	120	35.8	13.8	42.5	20.4	48.1	22.4	35.3
	125 up	88	121.7	61.8	285.0	102.9	219.0	53.3	104.6
DIAMETER	0-0.19 cm	13	0	....	0	0	0	0	0
	0.20-0.39	139	0.1	0.6	0	1.5	10.1	0	2.1
	0.40-0.59	174	4.4	5.1	23.5	26.0	26.5	6.2	15.3
	0.60-0.79	102	50.4	13.0	71.9	41.7	98.2	45.0	53.3
	0.80-0.99	43	97.9	166.0	285.0	148.2	120.0	36.1	142.4
	1.00 up	21	164.8	174.0	....	223.0	201.0	108.6	174.3
AGE	1 year	114	0.7	2.5	0	0.9	17.8	3.0	4.1
	2	116	21.1	4.3	4.7	23.4	62.1	3.6	19.9
	3	45	6.2	3.3	0	34.8	64.8	22.1	22.2
	4	67	28.0	4.6	18.9	60.5	33.8	15.3	26.9
	5	114	87.0	39.0	54.9	60.0	74.3	59.5	62.5
	6 up	37	101.8	18.3	....	....	134.2	46.9	75.3

ing from 42.2 to 85.7%. The fate of some of the buds which failed to set fruits is mentioned above. Many of the fruits which mature do not contain sound nutlets, however. Numbers of filled nutlets in normal-appearing fruits of the current season crop were determined in October 1949. An average of approximately half ($48.8\pm4.5\%$) of the nutlets were defective, the extremes among different widely separated colonies in the Minneapolis area ranging from 9.4 to 76.0%. There was about an equal distribution of fruits with two normal nutlets, fruits with one normal and one defective nutlet, and fruits with two defective nutlets. By far the majority ($58.1\pm4.4\%$) of the defective nutlets were empty although of normal size. The next largest category ($21.8\pm3.3\%$) was composed of nutlets the endosperm of which was white, dry, and floury-appearing and showed large visible air pockets. Nutlets with a dry and woody or pithy-appearing endosperm comprised $7.2\pm1.8\%$ of the total, while those in which a normal-appearing endosperm had so shrunken away from the still expanded endocarp as to occupy less than two-thirds of its original volume occurred in $6.0\pm2.0\%$ of the cases. Flat nutlets, or those in which even the endocarp never expanded, composed $6.9\pm1.8\%$ of the defective nutlets.

The causes of defection are not clear, but could result from failure of pollination, defective pollen or ovules, embryo abortion, self-incompatibility, or other conditions. Some evidence suggests that the proportion of defective nutlets tends to increase while the fruits remain attached to the shrubs. Furthermore, it was also observed that the common box-elder bug *(Leptocoris trivittatus* Say) sometimes feeds upon the maturing fruits with its long sucking mouthparts. Under experimental conditions it was shown that this insect will penetrate mature fruits with its mouthparts and feed upon the endosperm of the nutlets, which them becomes white, dry, and floury-appearing. Sucking insects are probably but a minor cause of defection, however, since they were observed to feed only occasionally on the fruits.

The fruits seem quite resistant to frost. A period of two weeks of very wet weather in late summer resulted in much cracking of the exocarp and mesocarp, but no other ill effects of rain, hail, or wind on the fruits were observed. Some effects of fire on fruiting behavior were observed on the same area burned in April which is described above, and compared to an adjacent unburned area. Although the fruit production on the burned area was only one-sixth that of the adjacent unburned plot in the year in which the fire occurred, it is remarkable that fruiting occurred at all. Fruit production during the second year, however, did not appear to be appreciably improved over that during which the fire occurred. Viability tests by embryo excision were made on dry fruits attached to fire-killed stems, and showed the nutlets to have been unharmed by the fire. On the other hand, oven heat tolerance tests of extracted and dried nutlets with a moisture content

of 8.2% demonstrated that exposure to 100° C for
five minutes is fatal to the nutlets. Fruit production
does not appear to be sensitive to soil fertility.
Plants were observed to fruit at least as heavily in
very infertile sand as they do in soils of intermediate
or high fertility.

There are several biotic agents which are signifi-
cant in their effects on the fruits which remain on the
shrubs after maturity. The box elder bug is men-
tioned above. A large proportion of the fruits in
1949 became visibly infested with a pulp-eating DIP-
TERA larva (Agromyzidae) as they approached
maturity. The insect does no harm to the nutlets, but
feeds only on the mesocarp of the fruit, resulting in
its rapid softening and decay. As is mentioned in
certain sections above, livestock, birds, rabbits, deer,
and especially mice may destroy many fruits, only
incidentally disseminating a few.

SENESCENT STAGE

DECLINE

It is difficult to detect evidence of decline or senes-
cence resulting from age in either colonies or indi-
didual stems of S. occidentalis. Physiological old
age is, in fact, probably non-existent in a species
which reproduces vegetatively as strongly as does
the one under consideration. Colonies quite conceiv-
ably might be able to maintain their individuality
much longer than the life duration of any single
stem, rhizome, or root, as a consequence of the con-
tinuous production of these organs. The symptoms of
low vigor in this species, which might be assumed to
be expressions of senescence, are most likely a conse-
quence of unfavorable environmental conditions.
These conditions may be externally controlled or pro-
duced indirectly by the dense colonies themselves
through their action on the soil biota or chemistry.
The former possibility is exemplified by a closing
overstory shading out and weakening formerly vig-
orous colonies, as at Station 16 mentioned above. The
clumps themselves do not apparently tend to change
the soil conditions in an unfavorable direction, for
the centers of colonies were observed to remain vig-
orous, not tending to die out with age. The oldest
wolfberry stems observed were still bearing fruits
abundantly and showed no signs of senescence.

LONGEVITY

The mean maximum stem age observed for all
twenty localities examined in Minnesota was 7.2±1.7
years, ranging from 3 to 13 years. The rhizomes nor-
mally attain a much greater age than do the stems.
The mean maximum rhizome age for the stations
examined was 18.9±3.3 years, and ranged from 5 to
40 years. The discrepancy in the ages of stems and
rhizomes is partly explainable by the periodic oc-
currence of fire, browsing, trampling, climatic ex-
tremes, and other factors which are much more de-
structive to erect stems than to the better protected
rhizomes. In addition, perhaps the stems are inher-
ently shorter-lived than the underground parts.

SUMMARY

ECONOMICS AND DISTRIBUTION

Symphoricarpos occidentalis, commonly known as
wolfberry or western snowberry, is a characteristic
and common clump-forming shrub in the great plains
and adjacent regions of the northern United States
and Canada. In Minnesota the species is common in
the former prairie and hardwood districts but is in-
frequent in the coniferous forests of the northeastern
part of the state.

Indians made limited use of S. occidentalis for a
variety of purposes. The shrub is considered a valu-
able livestock browse in the western part of its range,
but is a serious pasture weed in the eastern and
northern areas. Wolfberry is an important honey
plant, and is rated highly for wildlife food and
cover and erosion control.

Within much of its range S. occidentalis is a char-
acteristic component of the shrub layer of open
woods, of the forest-prairie ecotone, of chaparral, of
pastures and disturbed areas, and of open prairie and
plains. The species appears to be an important
factor in the replacement of grassland by forest or
scrub, since it is one of the few woody plants which
can invade dense grassland (by means of rhizomes)
in such quantities as to shade out the grasses and
favor invasion by taller shrubs or trees. In Minne-
sota and other humid parts of its range S. occiden-
talis appears to spread under conditions of grazing
or upon opening up of the forest, and hence is par-
ticularly characteristic of pastures.

The species occurs naturally only in climates of a
strongly continental type. Although the shrub usu-
ally occurs in full sun it also commonly grows in
the moderate shade of open woods. In the drier parts
of its range S. occidentalis grows most frequently in
relatively moist sites, such as north facing slopes,
ravines, depressions, and stream flats. In regions of
moister climate the species seems to occur more
commonly on south facing slopes and exposed bluffs
and hillslopes. Both tendencies are exhibited in dif-
ferent parts of Minnesota, depending upon precipita-
tion, soil, and competition. Wolfberry occurs on a
wide variety of both mature and immature soils vary-
ing from sand to clay. It has not, however, been
reported to occur on either very acid (below pH 6.1)
or saline substrata, on organic soils, or on soils which
are permanently saturated. Relatively poorly drained
soils, however, such as annually flooded stream flats,
are tolerated by the shrub.

LIFE-HISTORY

Unless eaten by birds or mammals the whitish
berry-like fruits (actually drupes) tend to remain
attached to the shrubs for a year or more, usually
falling in the spring or summer seasons. Certain
birds and mammals are probably the main dispersal
agents, since passage through their digestive tracts
may be survived by a proportion of the seeds (ac-
tually nutlets).

The nutlets of S. occidentalis have a double dor-

mancy, requiring for germination the breakdown of the coats plus the after-ripening and development of the embryo. In nature the coat restrictions are eliminated by fungal breakdown during storage in moist warm soil during the summer, occasionally hastened by passage through a bird or mammal digestive tract. After-ripening and development occur during one or more winters in the soil, and must be preceded by fungal breakdown of the coats. Artificially, acid treatment followed by refrigerator storage will permit germination. Extended periods of soil storage of viable nutlets are probably uncommon in nature since 99% of the nutlets recovered from the soil were found to be either empty, decayed, or opened by mice.

Germination occurs readily only between about 5° C and 15° C, and alternating temperatures are not appreciably more favorable than constant conditions. The process does not seem to require good aeration. In nature germination begins as soon as the soil thaws in early spring, none occurring in late spring, summer, or fall.

Young plants are quite sensitive during their first year to drought, certain invertebrates, and damping-off fungi, listed in decreasing order of importance found during the period of study.

At maturity stems of *S. occidentalis* in Minnesota average about 75 cm in height, being tallest on the moister sites and near the centers of colonies. Colonies vary from one to several hundred meters in diameter, often extending as a narrow belt along the edge of a forest or the banks of a stream. The stems near the center of a colony may be dense enough to shade out all herbaceous growth, especially on the moister sites, or they may be sparse throughout the colony. Long photoperiods appear to stimulate shoot growth. The cold temperature requirement of shoot buds necessary for their opening is not very great and would nowhere limit the present natural distribution of the species.

The roots of mature colonies usually arise in pairs along the rhizome nodes, one root below each paired bud. Some develop into main roots which penetrate deeply, to at least 155 cm in loamy sand, and branch profusely. The tips appear strongly mycorrhizal.

The flexible stems of mature colonies may be bent to the ground by snow, glaze ice, or winds, or may be frozen in solid ice without harm, but there is some evidence of winter-killing in Minnesota. Although the stems are easily killed to the ground by fire they resprout profusely from below the ground level. No insects or fungi attacking the vegetative parts were of importance during the period of study. The species is generally resistant to browsing and trampling by livestock, largely as a consequence of its relative unpalatability and rhizomatous growth habit. Attemps to eradicate the shrub from pastures have not been very successful.

In contrast to seedling production *S. occidentalis* reproduces vigorously by rhizomes. These tend to be long and sparsely branched, and occur from practically at the surface of the soil down to 35 cm. Over four times as great a length of rhizomes may be produced as length of main aerial stems. The rhizomes appear relatively free from injury by external factors. The shrub can be propagated readily by hardwood cuttings of the dormant aerial stems as well as by other methods

The flower buds appear as the end of the spring flush of growth approaches, and the flowering season extends for several weeks within the period from late May to mid-September. Experiments indicate that days longer than at least 14 hours are essential for flower bud initiation, but not for their subsequent development or anthesis. Photoperiod, however, probably nowhere limits the present natural range of the species. The temperature range tolerated for flower bud development and flowering is very wide. The nectar-bearing moderately showy and fragrant flowers are visited by both long and short tongued Hymenoptera, in addition to a number of Lepidoptera, and are thus relatively unspecialized as to insect pollinators. No special mechanisms tending to favor cross-pollination or discourage self-pollination are present. Partial self-incompatibility, however, may be present, but parthenocarpy or apomixis are not exhibited. A number of injurious insects feed upon flower buds and flowers, and a fungus destroyed large numbers of flower buds during 1949.

Fruit maturation does not have narrow photoperiod or temperature limits. Production appears to be generally heavy, tending to be greatest near the center of a colony, and to increase with increasing height, diameter, and to a lesser extent, age of the individual stem. Fire or cutting during the dormant season reduces but does not eliminate the production of fruits during the immediately following growing season, even if the stems are killed to the ground. Approximately half the nutlets produced appear to be defective, probably resulting from several causes. Fruits are quite resistant to frost, but the mature dry nutlets cannot survive fire temperatures which are over 100° C for even five-minute periods. Certain insects, birds, deer, livestock, rabbits, and especially mice feed upon the fruits or nutlets, only incidentally dispersing a few.

Stems are not as long lived as are rhizomes, the maximum stem age averaging about 7 years in Minnesota while the rhizomes average almost 20 years. The oldest stem examined was 13 years and the oldest rhizome 40 years. Both stems and rhizomes often remain vigorous up to their maximum observed age, and the older parts of colonies do not tend to die out with age.

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A CONSIDERATION OF CLIMAX THEORY: THE CLIMAX AS A POPULATION AND PATTERN

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INTRODUCTION

The approach to vegetation often described as "dynamic ecology," the central concepts of which are succession and the climax, was developed by Cowles (1899, 1901, 1910, 1911), Clements (1904, 1905, 1916), and Cooper (1913) as a major contribution of American ecology. The antecedents (Cowles 1911, Clements 1916) were almost entirely European (King 1685, Biberg 1749, Dureau de la Malle 1825, Kerner 1863, Hult 1885, Warming 1891, 1895, 1896, Flahault & Combres 1894, Graebner 1895, Meigen 1896, Drude 1896, Schimper 1898, etc.). In spite of these the viewpoint as stated by Clements (1916), especially the "monoclimax" or single climax of a given area, was received with a certain coolness by some authors on the Continent (Gams 1918, Du Rietz 1919, 1921:97, Domin 1923) while being applied with more or less modification by others. Among the Swiss-French or Zürich-Montpellier group, theory and practice have tended to resemble those of the Americans, (Braun-Blanquet & Furrer 1913, Rübel 1913, 1922, Lüdi 1920, 1921, 1923, 1929, 1930, Furrer 1922, Braun-Blanquet & Jenny 1926, Braun-Blanquet & Pavillard 1928, Braun-Blanquet 1928, 1932, 1933, 1951, Lemée 1937-9), but with climax and succession somewhat less emphasized in the conception of vegetation than by American authors. In Braun-Blanquet's treatment (1928, 1932, 1951) the development of vegetation in a given area tends toward the climatically determined end community (*klimatische*

Schlussgesellschaft) or climax. A single climax thus exists in a given climatic region, although other permanent communities *(Dauergesellschaften)* determined by other factors in addition to climate may occur there also; these would be termed sub- or proclimaxes in the American monoclimax conception. The grouping of successional communities related to the same climax forms the *Klimax-Komplex*, which corresponds to a geographic territory, the *Klimax-Gebiet*, conceptions approximately equivalent to the climax formation of Clements but free from the organismic analogy of Clements which interprets succession to the climax as growth to maturity of the climax formation as an organism.

Among the Scandinavian and Baltic plant sociologists emphasis of succession in the general interpretation of vegetation has been still less, although such more concrete successions as those of bogs, shores, and moraines have been intensively studied; and dissent from the monoclimax has been more pronounced (Du Rietz 1921, 1924, 1930b, Nordhagen 1928, Lippmaa 1933b, Faegri 1937). In some of the intensive vegetation monographs of this group the climax receives passing mention, if any, although the climax concept may be traced back to Hult (1885) and Warming (1896). While the monoclimax is rejected by Du Reitz, the conception of a major community or dominating coenose (Du Rietz 1930b:344, Faegri 1937, cf. the *Hauptcoenose* of Schmid 1922, 1935) without the assumption of convergence of other communities to this dominating coenose, is related to the prevailing climax discussed below. Nordhagen also rejected the convergence to a single climax, but recognized the major community of a given zone as a *regionale Hauptassoziation*, with which may occur an *edaphische Hauptassoziation* corresponding to the American physiographic climax or subclimax (Nordhagen 1928:526). Lippmaa in Estonia suggests a

similar conception of the climax as the stable com-
munity of greatest extent in an area (Lippmaa
1933b:22) but rejects the distinction between cli-
matically determined and edaphically determined
permanent communities, since all communities are
both edaphically and climatically determined (1933b:
43). Only stable communities are regarded as valid
associations, and these are distinguished as undis-
turbed *primary associations* and disturbed or modi-
fied but stable *secondary associations* (Lippmaa
1933a, 1933b, 1935a).

These two major groups of Continental plant so-
ciologists have in some ways followed Warming and
Cowles more than Clements; and it might be gen-
eralized, with some simplification of the matter, that
they have tended to treat succession within the frame-
work of their community classification, while the
Americans have tended to treat community units
within the framework of a successional conception
(*vide* Lüdi 1923:297). A contributor to climax the-
ory from Germany and the Netherlands, Tüxen, has
followed Zürich-Montpellier in part (Tüxen 1928),
but is also author of the concepts of the paraclimax
(Tüxen 1933, 1935) in its more widely used sense
corresponding to the edaphic subclimax of Clements
(Grabherr 1936) and the climax-group and climax-
swarm (Tüxen & Diemont 1937) of polyclimax impli-
cation. Another quite distinctive nomenclature of
climax and succession has appeared among some of
the authors of southern Europe (Del Villar 1929a,
1929b, Gaussen 1933, Cuatrecasas 1934, Ciferri 1936,
Trochain 1940) and was carried to its far point by
Ciferri with the recognition of eleven climax terms.
The climax of an area is conceived by Del Villar as
the *conclimax*, a complex or mosaic of climax asso-
ciations.

Ecological problems of the plains of Russia re-
semble those of the plains of North America, which
influenced the Clementsian monoclimax theory; and
a Russian monoclimax conception developed in close
relation to Russian soil science and somewhat inde-
pendently of American ecology (Alechin 1926, Walter
1943). In this conception zonal, extrazonal, and in-
trazonal or azonal communities correspond to cli-
matic climax, pre- and postclimax, and subclimax
communities but are preferred for their freedom
from the assumption of succession (Walter 1943:29).
The Russian viewpoint was much influenced also by
the concept of the steady-state applied to self-main-
taining vegetation (Ramensky 1918, Elenken 1921,
Iljinski 1921, Alechin 1926, 1927, Stantschinsky
1931). The steady-state conception has been rejected,
however, on the basis that "Instead of equilibrium,
the dialectical method suggests unity, divergency and
the struggle of contradictions (Lenin)" and the
further conclusion that "'While studying the suc-
cession of cenoses, we have to overcome both the
static fossilized conception of European phytocenolo-
gists and the somewhat fatalistic theory of succes-
sions of American scientists." (Bukovsky 1935:98)—
a way of thinking that is suggestive of what has

happened in other fields of biology. The distinguished
Russian author Alechin has indicated that the later
period of Russian phytocenology has been charac-
terized by (1) theoretical study of the fundamental
conceptions of the science and (2) reconstruction of
Russian phytosociology on the bases of the metho-
dology of Marx and Lenin (Alechin 1946, Roussin
1948), with the apparent assumption that these two
pursuits are compatible.

Development of climax conceptions in England was
influenced by Warming's concept of the *Schlussverein*
(1896) through Moss (1907, 1910), who distinguished
climax and seral communities as chief and subordi-
nate associations, and by Crampton's (1911, 1912)
concepts of stable and migratory formations. From
these sources and a strong influence of Clements and
other Americans the British "polyclimax" position
developed under the leadership of Tansley (1911,
1920, 1929, 1935, 1939; 1947-8). The British poly-
climax majority viewpoint was close to that of some
Americans following Nichols (1917, 1923), but the
prevailing American view has been that of the mono-
climax. Clements' own full formulation of this theory
was published in 1936 (also in 1949); and concep-
tions similar to those of Clements have been stated
by Phillips (1934-5), Weaver & Clements (1929),
Cain (1939), Dansereau (1946), Braun (1950), etc.,
and have been generally accepted by ecologists of the
"biotic" school (Shelford 1932, Woodbury 1933, Shel-
ford & Olson 1935, Clements & Shelford 1939, Car-
penter 1939). The Clementsian monoclimax concep-
tion, though widely criticized, has been most char-
acteristic of American ecology in the past and is
still an active and influential viewpoint, appearing
almost without qualification in current texts (Mc-
Dougall 1947, Oosting 1948), as well as in more ad-
vanced studies. The divergent interpretations of cli-
max and succession in America and elsewhere (Han-
sen 1921, Scharfetter 1921, Gams 1923, Cooper 1926,
Gleason 1927, Godwin 1929, Bourne 1934, Davis 1936,
Oberdorfer 1937, Walter 1937, Wood 1939, Tutin
1941, Graham 1941, Beard 1946, Cain 1947, Crocker
& Wood 1947, Beadle 1951, and citations above) have
led to a degree of confusion in the variety of ap-
proaches and units of treatment, indicated in Du
Rietz (1930a), Conard (1939), and Cain's climax
discussion of 1939.

Something of the nature of this confusion may be
illustrated by the profusion of climax terms in the
literature. Beginning with Clements' climatic climax,
subclimax, preclimax and postclimax, and potential
climax (1916), the climax terms have led through the
proclimax (1934), disturbance climax or disclimax,
serclimax, eoclimax, and panclimax (1936), edaphic
and physiographic or topographic climaxes (Nichols
1917, 1923), fire climax (Tansley & Chipp 1926) or
pyroclimax (Roberty 1946), aquatic climax (Wood-
bury 1933), biotic climax and anthropeic climax
(Tansley 1935), anthropoclimax (Tüxen & Diemont
1937), or archeological disclimax (Wells 1946), para-
climax (Del Villar 1929, Tüxen 1933), conclimax,

anteclimax, and peniclimax (Del Villar 1929), trans-
climax, metaclimax, and euclimax (Ciferri 1936), de-
flected climax (Marshall 1934) or plagioclimax
(Tansley 1935), pseudoclimax (Ciferri 1936, Car-
penter 1938) and quasiclimax (Tansley 1939, Dan-
sereau 1946), co-climax (Wood 1937), pedoclimax
(Lemée 1937–9:501), and salt-spray climax (Wells
1939) to, inevitably, the superclimax (Muller 1940).
Onward the march of science. A significant difference
in climax interpretation has, further, been described
in the monoclimax and polyclimax theories (Du
Rietz 1930a, Bourne 1934, Tansley 1935, Cain 1939).
In the light of the distinguished succession of climax
terms it is hoped that the present view will not be
known as the anticlimax hypothesis. Such a multi-
plicity of terms, many of them clearly exceptions to
the concept as originally formulated, may imply that
the concept is being stretched this way and that to
cover evidence for which it is not actually adequate.
If an ideal, the climax, must be so modified in appli-
cation, it may be suspected that the ideal is at fault.
The vagueness of usage has led Egler (1947) to
abandon the term "climax," regarding it as no longer
useful. Usefulness of the term and of the concept it
represents should be examined, primarily on the basis
of two questions: (1) Can the climax state be mean-
ingfully interpreted, defined, and measured as distinct
from succession? (2) Does the concept serve a useful
function in synecological research?

In the problems to be discussed, and in the history
of the climax concept, two approaches to climax
definition may be distinguished. Much of the con-
sideration of climax vegetation, and much of the logic
of the monoclimax, have been based on the physiog-
nomy, or structure in terms of growth-forms, of vege-
tation and its relation to climate. This area of vege-
tation problems, in the overlap of synecology and
geography, has been the subject of an extensive lit-
erature from some of the beginnings of plant ecology
to the present, indicating the adaptive or epharmonic
relation of climax vegetation to environment in terms
of both morphological life-form, vegetative form, or
growth-form (Humboldt 1806, 1807, Grisebach 1838,
1872, 1877, Kerner 1863, Drude 1890, 1913, Schim-
per 1898, 1903, Schimper-von Faber 1935, Warming
1895, 1896, 1909, 1933, Rübel 1930, 1936, Stefanoff
1930, Küchler 1949, 1951, Dansereau 1951; review
and dissent, Du Rietz 1931) and the Raunkiaer life-
forms (Raunkiaer 1910, 1934, 1937, Smith 1913,
Paulsen 1915, Hansen 1928, 1930, 1932, Braun-Blan-
quet 1932, Gelting 1934, Clapham 1935, Jones 1936,
1938, Allan 1937, Adamson 1939, Cain 1950, Danse-
reau 1951). It will be treated here as a necessary part
of climax theory, but not as the primary concern. The
other approach is to the climax as a population of
plants and animals of different species, with treatment
of natural communities in much greater detail than by
physiognomy alone. Synecology or biocenology is the
science of natural communities or, more broadly con-
ceived, the study of ecosystems (Tansley 1935, 1939:
228) and in its analytical aspects appears to center in
problems of populations and productivity in relation

to environment. Interpretation of the climax in
terms of populations and productivity thus may be
sought. It is felt that if the climax has real mean-
ing for analytical synecology, that meaning is pri-
marily in the climax as an object of and basis for re-
search treating populations and the productive or
metabolic dynamics of communities. The author has
sought, on the basis of theoretical considerations and
of his own field work in population analysis of nat-
ural communities, to formulate the climax concept in
a manner general enough to provide for the evidence
available and to give it functional meaning for ana-
lytical ecology. He has sought also, in stating the
interpretation developed, to draw together citations
of previous contributions to climax theory and of
some fraction of the world literature of vegetation
bearing on the problem as evidence.

EVIDENCE

Some evidence bearing on succession and climax
problems may be summarized as a basis for inter-
pretation:

1. Succession. The succession of populations on
disturbed or newly exposed sites is one of the best-
established phenomena of ecology, circumstantial as
most of the evidence is. The most effective demon-
strations of the manner in which populations suc-
ceed one another are in such short-range, small-scale
successions as those of infusions (Woodruff 1912,
1913, Allee 1932), carrion (Fuller 1934, Holdaway
1930), rotting logs and stumps (Shelford 1913,
Blackman & Stage 1924, Krogerus 1927, Savely
1939), dung (Mohr 1943), etc. While effective popu-
lation treatments of succession in the literature are
limited, evidence available indicates: (a) that the
flow of populations is often quite continuous through
and between the stages of succession (data of Cooper
1922a, 1923, 1939, Sampson 1930a, Faegri 1933,
Braun 1936, Vaughan & Wiehe 1941, Lüdi 1945,
Dansereau 1946, Eggeling 1947, Quarterman 1950,
Curtis & McIntosh 1951, Brown & Curtis 1952);
(b) that successions of the same general type toward
the same climax are variable in rate of change of
populations, both between different stages in the same
succession and in consequence of local climatic and
edaphic differences (Faegri 1933); (c) that succes-
sions are variable in composition of the stages, en-
vironmental differences causing different successional
populations to appear in similar successions in the
same area (Watt 1923-5, Kell 1938, Oosting 1942);
(d) that the changes may be irregular, shifting back
and forth because of environmental fluctuation (data
of Weaver & Bruner 1945), (e) that successions are
often telescoped (Cooper 1916), with the course of
succession variable because of chance differences in
what populations enter the succession at what time,
whole apparent stages being either skipped or added.
Evidence of successional irregularity is familiar
wherever stages of succession may be reasonably as-
sumed to appear along a spatial gradient, as around
an aging pond or bog, or a meadow being invaded by

forest. A meadow into which the forest is advancing in the Siskiyou Mountains, for example, may be ringed with shrubs; but the shrub stage is highly irregular, appearing in one place as a dense and solid belt, in another as scattered patches of various species, and being absent from other parts of the edge. Where a shrub thicket occurs it may be dominated in one place by Douglas maple *(Acer glabrum* var. *douglasii* (Hook.) Piper) and in another by alder *(Alnus tenuifolia* Nutt.); the patchy shrubs are dominated by various combinations, differing from place to place, of *Corylus rostrata* var. *californica* A. DC., *Holodiscus discolor* (Pursh) Maxim., and *Salix* sp., and with different representations of several minor species. Where the shrubs are absent, young trees *(Abies concolor* Lindl.) are invading the meadow directly; where there are shrubs the tree seedlings may appear ahead of or behind the densest shrubs, or they may be scattered ahead of the whole shrub belt.

Succession may thus be thought to occur, not as series of distinct steps, but as a highly variable and irregular change of populations through time, lacking orderliness or uniformity in detail, though marked by certain fairly uniform over-all tendencies. In its continuity and irregularity, and in the sharing of populations in different combinations by different successions, succession is effectively represented by Cooper's (1926) image, after Vestal, of a braided stream (cf. Alechin 1925).

2. Climax convergence. The conception of convergence of successions to the climax was fundamental to the early formulations of Cowles and Clements and is familiar on the levels of both physiognomy and population. Physiognomic convergence on a world-wide scale in the similar climates of different continents is a basis of the literature recognizing this phenomenon in terms of formations, formation classes (Warming 1909, Brockman-Jerosch & Rübel 1912), formation types (Nichols 1917, Schimper-von Faber 1935, Burtt Davy 1938, Tansley 1939:229, Dansereau 1951), isocies (Gams 1918), formation-groups and panformations (Du Rietz 1930a), homologous formations (Braun-Blanquet 1932), panclimaxes (Clements 1936), biochores (Hesse *et al* 1937, Dansereau 1951), biome types (Allee *et al* 1949, Tischler 1951). Convergence of seres within an area to the same physiognomy is also familiar; most successions in a forest area will lead to forest, most in a grassland area to grass. A degree of convergence appears also on the population level. On similar sites at least, within an area, similar climax populations are likely to be found.

3. Climax patterning. Because different population combinations appear in the different environments of any area, vegetation forms a complex pattern of plant populations. While some studies have attempted to draw all the vegetation types of an area into a successional schema, there are many studies showing the real complexity of patterning of stable vegetation (Stamp 1925, Petrie *et al* 1929, Trapnell

1933, Conard 1935, Meusel 1935, Potts & Tidmarsh 1937, Tansley 1939, Wood 1939, Falk 1940, Daubenmire 1942, Braun 1942, 1950, Crocker & Wood 1947, Watt & Jones 1948, Morison *et al* 1948). Even if the monoclimax theory is accepted, it may be recognized that diversity of species combinations is usually characteristic of the climax (Gilliland 1938).

Various topographic-edaphic effects (Shreve 1915, 1927, Brough *et al* 1924, Rohlena 1927, Cottle 1932, Meusel 1935, Braun 1935b, Bauer 1936, Gillman 1936, Tüxen & Diemont 1937, Potts & Tidmarsh 1937, Raup 1938, Bayer 1938, Steyermark 1940, Cline & Spurr 1942, Oosting 1942, Cobbe 1943, Williams & Oosting 1944, Buechner 1944, Boyko 1945, Egler 1947, Miller 1947, Sears 1947, Lüdi 1948) may result in a mosaic of climax types in an area. Breakdown of the climatic climax in mountain topography was indicated within American ecology as early as 1914 by Shreve (1914a:106), as the same author suggested the breakdown of the association the following year (1915:111). Edaphic factors have been the basis of many objections to the monoclimax theory (Tansley 1916, 1935, Nichols 1917, Bourne 1934, Michelmore 1934, Gillman 1936, Richards 1936, Milne 1937, Walter 1937, Wood 1939, Steyermark 1940); and references to edaphic factors occur throughout the literature, such effects apparently being observed in every vegetational area studied with sufficient intensity. The soil moisture factor is universal in its effect on vegetation, appearing in the form of swamp and marsh, flood-plain and ravine "serclimaxes" and "post-climaxes" (Ainslie 1926, Swanson 1929, Grant 1934, Marshall 1934, Clements 1936, Little 1938, Cain & Penfound 1938, Tansley 1939, Richards 1939, Beaven & Oosting 1939, Trochain 1940, Tolstead 1942, Fairbairn 1943, Eggeling 1947, Zohary & Orshansky 1947, Hotchkiss & Stewart 1947, Tchou Yen-Tcheng 1949, Beard 1949) as well as of alternes, etc., and in physical effects of soil texture and underlying strata on vegetation (McLuckie & Petrie 1926, 1927, Keller 1927, Botke 1928, Patton 1930, Barrington 1930, Shreve & Mallery 1933, McBryde 1933, Richards 1936, Davis 1936, Olmsted 1937, Kielhauser 1939, Shantz & Piemeisel 1940, Oosting 1942:111, McComb & Loomis 1944, Fautin 1946, Dyksterhuis 1948, Wilde *et al* 1948, Livingston 1949, Køie 1950, Platt 1951). Chemical effects of soil (so far as there is any meaning in the distinction between "physical" and "chemical" here) are also widespread (Weiss 1923, Firbas 1924, Keller 1925-6, Lämmermayr 1926, 1927, 1928, Domin 1928, Breien 1932, Schwickerath 1933, Flowers 1934, Soó 1936, Bjorkman 1937, Krist 1940, Johnston 1941, Birrell & Wright 1945, Zohary 1945, Rivas Goday & Box 1947, Wilde *et al* 1948, Pichi-Sermolli 1948a, Billings 1950, Zangheri 1950, Albertson 1950). A few further references may suggest that edaphic effects on climaxes, if not universal, appear on all continents and in all kinds of climates (Stamp & Lord 1923, Shantz & Piemeisel 1924, Shantz 1925, Haman & Wood 1928, Sukachev 1928, Cox 1933, Wilde 1932, 1933, Frey-Wyssling 1933, Killian & Dubuis 1937, Tüxen & Diemont 1937, Falk 1940, Pidgeon 1941, Zohary 1942,

1947, Seifriz 1943, Hou 1944, Marks 1950). The assumption that edaphic effects on vegetation are successional, that with soil maturity differences cease to be effective (Clements 1920, 1928:284-5, Brockmann-Jerosch 1925-9, Daubenmire 1947:55) may be rejected as by Beadle (1951) and many others accepting the polyclimax position. Edaphic factors, it would appear, are not special, local, and seral in effect, but are quite general in their contribution to vegetation patterning.

4. Climax continuity. That vegetation types are separated by boundaries called ecotones is a frequent assumption, but equally general is the observation that transition between two types may be very broad and gradual, so that it is impossible to recognize any real discontinuity. Continuous intergradation was indicated for the vegetation of the Faeröes by Ostenfeld (1908), and for the forest and grassland patterns of Bohemian mountains by Domin (1928a). McBryde (1933) has suggested that the vegetational response to a continuous climatic gradient is continuous, and Cooper (1942) has described vegetation of a transitional area in Alaska as a gradating pattern. Data of various authors (Frödin 1921, Linkola 1924, Hansen 1930, 1932, Sampson 1930b, Meusel 1935, Halliday 1935, Horton 1941, Spilsbury & Smith 1947, Marler & Boatman 1952) indicate the continuity of the types described. The author, in an attempt to determine the validity of eastern forest associations and ecotones in the Southern Appalachians, found population transition continuous through and between the traditional associations (Whittaker 1951, 1952). In studies of the Wisconsin forests during the same period by Curtis & McIntosh (1951) continuity was demonstrated and has been further developed for both forest and prairie (Curtis 1951, Brown & Curtis 1951, 1952, Gilbert 1951, Tresner 1951, Randall 1951). In vegetation forming "a complex continuum of populations" (Whittaker 1951) associations have only such subjective meaning as is consistent with the individualistic hypothesis of Gleason (Gleason 1926, 1929, 1939, Raup 1942, Cain 1947, Mason 1947, Egler 1947, Braun 1947, 1950, Whittaker 1951, 1952, Curtis & McIntosh 1951, Brown & Curtis 1952; dissents by Tansley 1920, Allorge following Lenoble 1926, Nichols 1929, Clements et al 1929:315, Phillips 1934-5). The "individualistic" conception appeared independently in France (Lenoble 1926, 1928, Fournier 1927), without being made welcome among phytosociologists, and in Australia (Patton 1930) and Russia (Ilínskii & Poselskaia 1929); and the conception of the vegetational mantle as being fundamentally continuous and without boundaries between recognized units was developed in Russia by Ramensky (Ramensky 1924, Roussin 1948). While there is some evidence and theory on the occurrence of discontinuities (Cajander 1909, Du Rietz 1922, 1924, Beauchamp & Ullyott 1932, Gause 1936, 1937, Pfeiffer 1943, Nytzenko 1948, Hairston 1951), it is suggested that usually climax populations change continuously along continuous gradients, observed

discontinuities being produced locally by either environmental discontinuities which telescope transitions or incompatibility of growth-forms or species which steepen the rate of change along a part of the gradient.

5. Climax irregularity. In spite of the convergence of climax populations on similar sites, no two stands are quite alike. Patchiness or irregularity is familiar on a smaller scale, within stands, in the herb and shrub layers of many vegetations, as in the prairie quadrat maps of Thornber (1901) and data of Steiger (1930) and the forest quadrat maps of Lippmaa (1935b), in bogs, vegetation of which in composition and micro-relief may form a mosaic of two or more phases (Osvald 1923, 1949, Lewis & Dowding 1926, Ljungqvist 1927-9, Rudolph et al 1927, 1928, Nordhagen 1928, Katz 1930, Yoshii & Hayasi 1931, Tansley 1939, Sjörs 1948), and in studies of contagion (Blackman 1935, Ashby 1935, 1948, Clapham 1936, Cole 1946, Archibald 1948, Greig-Smith 1952). Since some positive contagion or clustering appears to be general in natural communities, while negative contagion also occurs, a stand may be conceived (cf. Elton 1949) as a system of superimposed population lattices differing in density, spacing, degree of contagion, and degree of association with one another. Stand-to-stand irregularity is familiar in forests (Cooper 1913, Graham 1941, Maissurow 1941, Stearns 1949) and is indicated by association tabulations (Braun-Blanquet 1915, Allorge 1922, Frey 1922, Szafer et al 1924, Braun-Blanquet & Jenny 1926, Nordhagen 1928, 1943, Keller 1930, Mrugowsky 1931, Böcher 1933, Krajina 1933, Klika 1932, 1936, 1939, Schmid 1936, Mikyška 1939, Lüdi 1941, 1943, 1948). Such old and apparently stable vegetation as the Southern Appalachian cove forests (Cain 1943) and tropical and subtropical rain forests (Aubréville 1938, Fraser & Vickery 1938) vary strikingly from stand to stand, probably partly because of site differences, but also because of fluctuation in populations and chance differences in history of the stands. Environmental factors may cause irregularity, as in the California chaparral which is adapted to fire, but in which marked patchiness is produced by irregularity of burning (Bauer 1936), by small-scale soil differences affecting plant populations within a single stand (Kelley 1922, Stewart & Keller 1936), by such special edaphic situations as fallen logs and stumps, rocks and wind-fall pits, the "edaphids" of Sernander (Sernander 1936, Arnborg 1940), by surface waterflow patterns (MacFadyen 1950), by microrelief, as on till (Braun 1936, Chapman 1942) and other soils (Sampson 1930a), solifluction terraces (Troll 1944, Washburn 1947, Watt & Jones 1948, Metcalfe 1950) and other frost-determined landforms—tundra hillocks (Pohle 1908, Cajander 1913, Polunin 1935, Porsild 1938, Sharp 1942, Walter 1943, Troll 1944) and polygons (Zimmermann 1912, Högbom 1914, Summerhayes & Elton 1923, 1928, Huxley & Odell 1924, Elton 1927, Gates 1928, Regel 1932, Polunin 1934, Sørensen 1935, Russell & Well-

ington 1940, Walter 1943, Washburn 1947, Hopkins & Sigafoos 1951), stone stripes (Högbom 1914, Troll 1944), *Strangmoor* (Cajander 1913, Tanttu 1915, Auer 1920, Nordhagen 1928, Troll 1944), frost scars and peat rings (Hopkins & Sigafoos 1951). Irregularity of composition, within and between stands, may be thought a general characteristic of climaxes.

6. Climax instability. Spatial irregularity of populations is closely related to, and may be an expression of, underlying temporal instability. Theoretical considerations, developed primarily for animal populations (Lokta 1925, Volterra 1926, 1931a, 1931b, Bailey 1933a, 1933b, Nicholson & Bailey 1935, Smith 1935, D'Ancona 1939, Thompson 1939, Varley 1947), indicate that cyclic fluctuations of interacting species are to be expected under some conditions and are supported by experiment (Gause 1934a, 1934b, 1935, DeBach & Smith 1941, Utida 1950). Fluctuations of animal populations have been widely observed (Elton 1924, 1942, Uvarov 1931, Duffield 1933, Middleton 1934, Hamilton 1937, MacLulich 1937, Naumov 1939, Clements & Shelford 1939, Carpenter 1940, Dymond 1947, Leopold 1947, Siivonen 1948, Allee *et al* 1949, Shelford 1951), although these may be irregular and environmentally determined, rather than cyclic (Palmgren 1949, Cole 1951). These fluctuations occur within functioning ecosystems and may be thought expressions of, or contributions to, a more general instability of the ecosystems. Plankton communities, with their short life-cycles, offer a picture of instability which may be hidden by the longer life-cycles of major terrestrial organisms. The extreme instability of the plankton, with the populations changing rapidly, often in an apparently unpredictable fashion (Krogh & Berg 1931, Pearsall 1932, Riley 1940, Pennington 1941, Hutchinson 1944, Pennak 1946, 1949, Chandler & Weeks 1945, Verduin 1951) is suggestive, though perhaps exaggerated beyond the instability of terrestrial communities. Instability of marine littoral communities was described by MacGinitie (1939). In vegetation itself, environmental instability may permit only a relatively unstable climax, if it is regarded as such, as in frost-affected arctic terrain (Griggs 1934, 1936, Raup 1941, 1951, Sigafoos 1949, Hopkins & Sigafoos 1951) and active scree slopes (Hess 1910, Allan 1926a, Leach 1930). Climatic fluctuation may result in population change, as has been recorded for the American prairies (Weaver *et al* 1935, 1936, 1939, 1940, 1943, 1944, Albertson & Weaver 1942, 1944, Timmons 1941-2, Pechanek *et al* 1937) and is especially conspicuous in the annual vegetation of arid regions (Paczoski 1917, Alechin 1926, Chipp 1930, 1931, Talbot *et al* 1939, Went 1948, 1949, Went & Westergaard 1949, Zohary & Orshansky 1949, Shreve 1951). Changes in alpine vegetation in a decade were shown by Lüdi (1940). As the climax pattern is altered and shifted by climatic change, such conditions as those described by Blake (1938) of fluctuating climaxes of complementary communities oscillating in time and space and in the observation of Paczoski

(1917) of steppe and marsh vegetation alternating in time in the same place, may result. Fires may, in fire-adapted climaxes, produce population changes (Jarrett & Petrie 1929, Bauer 1936, Garren 1943, Sampson 1944, Hopkins *et al* 1948, Lemon 1949, Weaver 1951b). Reproduction may be periodic, depending upon especially favorable conditions, as in the English beech (Watt 1923-5), Finnish pines (Renvall 1912, 1919, Lakari 1915), etc. Stands may tend to stagnate until windfall, fire, or insect attack opens the canopy and permits new reproduction (Cooper 1913, Bergman 1924, Moss 1932, Sernander 1936, Poole 1937, Graham 1939, Maissurow 1941, Meyer & Stevenson 1943, Cline & Spurr 1942, Hough & Forbes 1943, Jones 1945, Stearns 1949). An irregular rhythm, sometimes involving different dominant populations, may thus be implicit in the manner of maintenance of the climax population; and cyclic processes have been observed in various vegetations, depending upon vegetational process (Nilsson 1899, Cajander 1904, Sernander 1910, Osvald 1923, 1949, Tansley 1939:683-695; Watt 1936, 1945, 1947a, 1947b, Tansley 1939:355, Godwin & Conway 1939, Coombe & White 1951), erosion in relation to succession (Bayer 1933), effects of animals (Cockayne 1909, Marler & Boatman 1952), and seasonal environments (Saxton 1922, 1924). From the evidence, particularly that summarized by Watt (1947b) and Jones (1945), it may be judged that a degree of instability, involving both response to environmental fluctuation and internal dynamics of communities, is characteristic of climax populations.

SUCCESSION AND RETROGRESSION

The term "succession" may with equal justice be applied to all vegetational change (Cooper 1926, Gleason 1927) or restricted to the shorter-range development to a climax on a given site (Iaroshenko 1946, Major 1951). The latter convention has been preferred here as permitting a clearer distinction of climax and succession. Fundamental to both succession and climax is the interplay of populations as these affect one another in such ways as either to change directionally in succession or to fluctuate about an average in the climax. In the development of a self-maintaining system of interacting populations, the climax community, from the less orderly seral populations, succession is an evolutionary process in the general sense (Wiener 1948). In the evolution of tides the diverse currents produced by gravitational forces are organized by environment, the ocean basin, into a definite tidal pattern. In organic evolution gene frequencies fluctuate with mutation and population changes, and with environmental selection there is progressive change in frequencies of some genes and change in the adaptive pattern of the species. The varied, experimental adaptive responses of childhood become organized in a manner determined, though not rigidly, in relation to conditions of environment into the personality

pattern of the adult. In these, as in ecological succession, there is progressive development of a pattern adapted to environment. The environment directs or fashions the development or evolution; the resulting pattern is an expression of its environment even though quite different patterns may correspond to, and perhaps be equally adapted to, a given environment. Adaptation, the matching of organic pattern with environmental pattern (Whittaker 1952), whether of the organism or community, is thus achieved and maintained through such evolutionary processes.

Certain trends or progressive developments toward the climax may characterize successional evolution. Community productivity tends to increase to a steady-state in the development of a terrestrial community, as in the aging of an aquatic one (Hutchinson & Wollack 1940, Lindeman 1942, Pennington 1943, Hutchinson 1948). Presumably, however, productivity is greater in a late seral stand than in the climax (Clements & Shelford 1939:116); energy activity in the developing community, as in a growing boy, may exceed the sustained level of the mature state. Decrease of productivity in the replacement of forest by heath led Lüdi (1923:295) to distinguish the optimal community of maximal productivity from the terminal community or climax in this succession. Along with increasing productivity, there is usually progressive increase in mass of the community structure (Del Villar 1929) as dominants of "higher" growth-form replace seral dominants, though some seral communities may be replaced by climax communities of smaller or "lower" growth-form. Soil depth increases through many seres, and the soil may develop to maturity in the climax; but this relation is by no means a necessary one, as indicated below. As early seral communities are simple and climax communities usually complex, there may be a progressive increase of community complexity, of diversity of species (Hansen 1930, Bojko 1934) and symmetry of community function (Park 1941), up to the climax. There would seem to be no reason, however, why in some cases, as in an open subclimax stand with rich undergrowth preceding a dense, closed climax stand, a seral stand should not be more complex and diverse than the climax. There may be increasing regularity of population distribution during the succession, as patchy, irregular seral stands are replaced by the more uniform climax stands (Cajander 1909); but there would seem to be no reason why some subclimax stands should not be at least as uniform as the following climax. The fact that species populations in succession may spread as clones or clans around a parent individual might imply that climax populations, when these species have had time to spread until identities of the clones or clans are lost, would show less contagion; but no clear difference in extent of contagion has appeared (Whitford 1949). The exceptions to all such trends through succession suggest considerable wariness in their application, but the exceptions should not obscure the significance of the trends themselves. In general, through the process of succession in terrestrial communities, there is progressive increase in community complexity and diversity, stature or massiveness and productivity, maturity of soil, and relative stability and regularity of populations.

Some vegetational developments are described as "retrogressive succession," but this paradoxical expression, a kind of oxymoron if succession is conceived as by Clements, requires definition if it is to be used with meaning. The possibility of retrogression in communities has been denied by Clements (1916) and Phillips (1934-5), while being defended on various grounds by others (Cowles 1901, 1919, Moss 1910, 1913, Cooper 1916, Gleason 1917, 1927, Nichols 1923, Bourne 1934, Tansley 1935, Buechner 1944). Open energy systems, such as those in which the various evolutionary processes occur, cannot actually run backwards although reversible changes may occur in them. A developing system is, as one author has described the human organism, "an arrow pointed through time in one way" (Wiener 1948:46). Clements' pronouncement that "Retrogression, an actual development backwards, is just as impossible for a sere as it is for a plant." (1928:147) is not in this case a pointless analogy. Changes can occur in these systems which are, by definition, retrogressive, however. Regression, as the term is used in psychiatric psychology, cannot imply an exact return to childhood traits (Conklin 1923:379, Mowrer 1939:61). If it is defined, however, that a loss of "genital" maturity (Freud 1935) or personal creativity or productiveness (Barker et al 1941) is to be regarded as regressive, as a turning back in those aspects of the personality, then such a development may be termed regression by definition.

If, in synecology, the mature or climax community is defined in terms of maximum diversity, productivity, soil maturity, stability, etc., then change in the community which involves decrease in one or more of these can be defined as retrogressive. Such changes may differ in character from the reversible changes discussed by Gleason (1927) as retrogression. It should be obvious that such a retrogression is not a return through past time but a turning back at an angle, in a direction different from the original development. Because of the unreliability of some of the criteria of community maturity, the decision as to whether a given change is retrogressive may be necessarily subjective. It may be more reasonable in many cases to speak of "deflected" development (Godwin 1929), indicating a succession in a direction different from that which might otherwise occur but with no implication of retrogressive character. When under severe grazing, however, the productivity of a community is gradually reduced, the soil impoverished and eroded, and the community simplified to a patchy, unstable population of weedy annuals, the change seems meaningfully retrogressive. Retrogression may be in some cases a useful term to describe changes occurring in a community, changes "retro-

gressive" by definition, and perhaps most significantly involving decrease in community productivity.

CHARACTERISTICS OF THE CLIMAX

Through succession the community develops from one of scattered pioneers utilizing only a fraction of environmental resources available, to a mature community with maximum utilization of resources on a sustained basis (Dansereau 1946). Energy of sunlight, converted into the available energy of organic compounds, is transferred through the several metabolic or energetic levels of the community with progressive degradation of energy which, however, is replaced by continued photosynthetic activity (Lindeman 1942, Allee *et al* 1949). Community activity in a lake, expressed as productivity, is determined, given sufficient light and water, by the inorganic nutrients available for protoplasmic synthesis, especially the one or more present in shortest supply relative to need, and by environmental temperature as it affects rates of activities, as major factors (Rawson 1939, 1942, Deevey 1940, Lindeman 1942). In terrestrial communities amount of water available to support transpiration of plants and other needs is a major determinant along with temperature and nutrients. We find in consequence the decrease in community mass, productivity (Jenny 1941:207), and photosynthetic efficiency (Lindeman 1942) along the moisture gradient from rain forest through other forest types, savannah, woodland, and shrub communities, and grasslands to desert. Along the temperature gradient from tropics to arctic a similar lowering of community productivity and stature appears; and, given a particular level of water supply and temperature, difference in nutrients may determine relative productivity of two terrestrial communities. The relation of environment to structure was expressed in the observation of Dansereau (1951: 219) that "an increasingly favorable combination of temperature and moisture permits increased closing, elevation, and differentiation into strata of the community." In its function, in utilization of energy supply in a manner determined by environment and characteristics of the system, the natural community, like the organism (Haskell 1940, Schrödinger 1946, Weiner 1948) has the characteristics of the counter-entropic, open energy system (D'Ancona 1939, Bertalanffy 1950a, 1951).

One characteristic of open energy systems is the possibility of equifinality (Bertalanffy 1950a, 1950b, 1951). Because material and energy drawn from environment are utilized and organized in a manner determined by the properties of the system itself, as well as in relation to environment, the end point of a development or evolution may be in part independent of its starting point. Essentially identical sea-urchins may develop from a whole embryo or from each of two half-embryos. Similar communities may develop in the conditions of a given site whether the development is a primary succession on exposed rock or a secondary succession following fire or other disturbance. As the final condition of the organism is determined by the organizing effects and interaction of the genes in partial independence of original condition, the final condition of the community is determined by the interaction of populations and their organization into a self-maintaining balance in partial independence of original environment and populations. The fact that similar climax communities may develop from differing initial conditions and may replace widely different seral populations is a striking example of open-system equifinality, and one in which the degree of independence of starting condition and course of development appears much greater than in the organism. The degree of independence of environment appears, in contrast, to be much less; for the developing natural community has no such built-in, determinate pattern as is provided by the genic system of an organism. As the productivity of the natural community is determined directly in relation to environmental conditions, and the populations in which this productivity is expressed are determined by population interactions in relation to environment, the dependence of the final characteristics of the community upon environment is more direct and immediate than in the organism. Thus, while the equifinality of the open system appears in both organism and natural community, the different organization of these two systems implies a contrast in the degree to which the equifinal state is independent of starting point and environment.

As one aspect of climax interpretation it may be said that the equifinal, climax steady-state represents a maximum sustained productivity or level of function for the environmental resources and conditions affecting community function (Lüdi 1921, 1923). Climax structure and function may be thought adapted to maximum productivity under given environmental conditions (Paczoski 1921, Alechin 1926, Sukatschew 1929), though the efficiency of utilization is necessarily determined by the kinds of organic populations making up the community. Given the same environmental conditions in two widely separated sites, as on different continents, there may be differences in productivity determined by the different kinds of organisms available to form the climax communities. The communities which develop are, however, organized wholes or systems showing such community properties as physiognomy, diversity, productivity, organization in terms of metabolic or energetic levels, spatial stratification, daily and seasonal periodicity, etc. As an organized system the community is a functional whole, showing emergent characters on its own level as does the organism (Phillips 1931, 1934-35, Egler 1942, Allee *et al* 1949), though radically different from the organism in its manner of organization. As an organic open system the community may be expected to express in its structure and function the conditions of its environment. Because of the intimate relation of structure and function (in spite of the artificial distinction enforced by lan-

guage) in adaptation, we may speak of the community's structural-functional pattern, its manner of operating together with the physical basis of its operation to utilize with maximum effectiveness the resources of environment in biological activity.

Some relations of structural-functional patterns of communities to environment are familiar enough in the many types of physiognomic adaptation described by Schimper, Warming, and others. If deciduous trees are better adapted to utilize the productive potential of a continental climate of wet summers and severe winters, evergreen trees better adapted to the maritime temperate climate of wet and moderate winters and dry summers, for this adaptive difference and for historical reasons also (Küchler 1946) we may expect to find the difference in dominance of these growth-forms so strikingly illustrated in the eastern and western forests of North America. It may also be observed that many stands of either area contain, and some may be dominated by, trees of the growth-form characteristic of the other; the difference is one of relative emphasis. Because different species may utilize the resources of the community in a manner complementary as well as competitive, maximum productivity can often be better maintained by a balanced pattern of several growth-forms than by a single growth-form. Individual species in a community tend not to meet in direct competition, as shown for animals (Lotka 1932, Volterra 1926, 1931a, 1931b, Gause 1934a, 1934b, 1935, Gause & Witt 1935, Hutchinson 1941, 1948, Lack 1944, 1945, 1946, Crombie 1945, 1947, Elton 1946, Hairston 1951, Williams 1947, 1951, Bagenal 1951) and indicated for the plant community by Shreve (1915: 112) and Alechin (1926). Stands approaching single-species composition most frequently occur in extreme conditions (Alechin 1926), while stands in favorable tropical environments are diverse (Whitford 1906, 1909, Seifriz 1923, Davis & Richards 1934, Richards 1936, 1939, 1945, Aubréville 1938, Holttum 1941, Beard 1946, Black *et al* 1950). Increasing impoverishment of communities may be expected with increasingly rigorous conditions (Cajander 1909), as in the decrease of plant species toward higher elevations (Tidestrom 1925:14, Davidsson 1946, Fries & Fries 1948), in relation to the moisture gradient (Linkola 1924, Hansen 1930, Whittaker 1952), and in the faunistic trends compiled by Hesse (1937:23-31, 144, 249). The more favorable the environment the greater the diversity of species populations and of growth-forms likely to be present in the community structure.

It is felt that the curves of of Fig. 1 are of some significance in illustrating, for the tree-stratum, the balance among growth-forms and the change in this balance with change of environment. In the most mesic valleys of the Great Smoky Mountains the cove forests (mixed mesophytic association) occur, with diverse stands of broad-leaved deciduous trees, among which few are fagaceous. As one moves along the moisture gradient from the cove forests toward
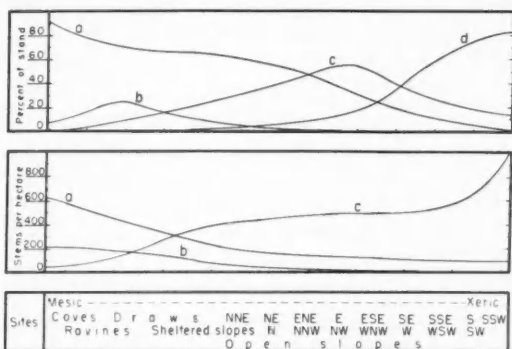

FIG. 1. Distribution of growth-forms of trees in relation to the moisture gradient at low elevations in the Great Smoky Mountains of Tennessee and the Siskiyou Mountains of southwestern Oregon.

Above, in the Great Smoky Mountains National Park, near Gatlinburg, Tenn., 13 stations along the moisture gradient using 37 site-samples for elevations between 1500 and 2500 ft. (data of Whittaker 1951); figures are percentages of stems over 0.5 in. d.b.h. in stand for: **a, deciduous-broadleafs** other than fagaceous and ericaceous species *(Halesia monticola* (Rehd.) Sarg., *Aesculus octandra* Marsh., *Tilia heterophylla* Vent., *Liriodendron tulipifera* L., *Betula alleghaniensis* Britt. and *lenta* L., *Acer saccharum* Marsh. and *rubrum* L., *Cladrastis lutea* (Michx. f.) K. Koch, *Cornus florida* L., *Hamamelis virginiana* L., *Nyssa sylvatica* Marsh., *Carya glabra* (Mill.) Sweet and *tomentosa* (Lam.) Nutt., *Magnolia* spp., etc.); **b,** an **abietine** *Tsuga canadensis* (L.) Carr.); **c, semi-sclerophyllous deciduous,** fagaceous *(Castanea dentata* (Marsh.) Borkh., *Quercus borealis* Michx. f., *montana* Willd., *alba* L., *velutina* Lam., *coccinea* Muench., *marilandica* Muench., *stellata* Wang., and *falcata* Michx.) and ericaceous *(Oxydendrum arboreum* (L.) DC., *Clethra acuminata* Michx.); **d, pines** *(Pinus strobus* L., *rigida* Mill., and *virginiana* Mill.).

Below, in the Siskiyou Mountains, on diorite, Oregon Caves National Monument, Josephine Co., Ore., ten stations along the moisture gradient using 50 site-samples for elevations between 2000 and 3000 ft.; figures are numbers of stems over 0.5 in. d.b.h. per hectare for: **a, needle-leaved evergreens** *(Chamaecyparis lawsoniana* Parl., *Pseudotsuga taxifolia* (Lam.) Britt., *Pinus lambertiana* Dougl., *Taxus brevifolia* Nutt.); **b, deciduous-broadleafs** x.33 (Cornus nuttalli Aud., Corylus rostrata var. *californica* A. DC., *Alnus rhombifolia* Nutt. and *rubra* Bong., *Acer macrophyllum* Pursh and *circinatum* Pursh, *Holodiscus discolor* (Pursh) Maxim., etc.); **c, evergreen-sclerophylls** x.33 *Lithocarpus densiflora* (H. & A.) Rehd., *Quercus chrysolepis* Liebm., *Arbutus menziesii* Pursh, *Castanopsis chrysophylla* (Dougl.) A. DC.), and *Quercus kelloggii* Newb., semi-sclerophyllous deciduous. The populations of deciduous and sclerophyllous species have been reduced to one-third of actual numbers for comparison with the needle-leaved trees as an approximate compensation for the larger size of the latter.

drier sites, the cove-forest species become progressively less important while first an abietine, eastern hemlock, increases and declines and then the fagaceous trees, chestnut and oak species, increase to become dominant in intermediate sites. Further along the gradient the pines are increasingly important, finally becoming dominant with decreasing propor-

tions of fagaceous trees and small numbers of the cove-forest species toward the xeric extreme. In the Siskiyous, conifers dominate the stand in mesic sites, but with a large deciduous fraction and a smaller evergreen-sclerophyllous one. Toward drier sites there is a progressive decrease of the conifers and deciduous trees relative to the sclerophylls until, on dry south slopes, the community is dominated by sclerophylls with an open coniferous overgrowth and a small fraction of deciduous species. Such a shift in balance among growth-forms is comparable to the progressive shifts in biological spectrum or balance among Raunkiaer life-forms shown along climatic gradients by various authors cited above and along local gradients by Linkola (1924), Cajander (1926), Hansen (1930, 1932), Halliday (1935), along local gradients and through succession by Oosting (1942). Different balances of growth-forms and life-forms may well be equally adapted to the same environment, even within the same area, as mesic sites in the Smokies may support stands dominated either by the conifer, eastern hemlock, or by a mixture of deciduous species. The tendencies in adaptation through growth-forms may be recognized, however; and the structural-functional pattern of the community may involve a balance among growth-forms, a balance changing continuously with change in environment or with local, partial discontinuity.

While the structure of the terrestrial plant community may be thought of in terms of growth-forms, it may also be considered in terms of populations; the structural-functional pattern of a natural community is necessarily one of species populations. "Stability" of these populations has traditionally been an attribute of the climax, but for stability may be substituted the concept of the steady-state, first applied to the plant community by Russian ecologists. If the climax has meaning as a combination of species populations, a degree of balance among these populations should exist in which, as energy and material move through the community, individuals are constantly being lost, but being replaced by reproduction at an equal rate on the average. The balance is a dynamic one, as effectively expressed in the terms *Fliessgleichgewicht* and *équilibre mobile*, an active equilibrium in which the populations tend, by their interplay in relation to environmental limitations, to keep one another within relatively stable limits. As the balance is a balance of populations in relation to one another and environment, difference in environment implies difference in balance (Nicholson 1933). Tabulations from the author's Siskiyou

TABLE 1. Numbers of stems per hectare of six major tree species on four directions of exposure in the Siskiyou Mountains, southwestern Oregon. Based on ten site-sample counts of 0.1 hectare each for each direction of exposure including all stems over 0.5 inch dbh.; samples taken on slopes with inclinations between 15° and 30° at elevations between 2000 and 3000 feet in the vicinity of the Oregon Caves National Monument on quartz diorite or other non-mafic and non-calcareous rock. Directions of orientation: NE=N, NNE, and NE; E=E and ENE; SE=ESE, SE, and SSE; S=S and SSW.

Species	*Pseudotsuga taxifolia*				*Chamaecyparis lawsoniana*				*Lithocarpus densiflora*			
Exposure	NE	E	SE	S	NE	E	SE	S	NE	E	SE	S
Stems per Sample	21	53	13	2					144	138	8	103
	12	16	10	43	51					115	151	19
	35	16	28	6	4				66	125	92	159
	12	17	19	15	10				13	245	77	46
	18	18	19	31	2				29	51	43	60
	57	12	9	16	23					78	41	141
	27	21	3	4	2				35	42	74	114
	19	13	15			2			106	123	16	62
	4	8	7						229	61	100	72
	9	8	8	12					60	196	56	98
Stems per H	214	182	131	129	92	2			682	1174	658	874

Species	*Quercus chrysolepis*				*Arbutus menziesii*				*Castanopsis chrysophylla*			
Exposure	NE	E	SE	S	NE	E	SE	S	NE	E	SE	S
Stems per Sample	28	3	75	17	19	3		10	27	58		8
			35	189		18	7	30	9	32		
	1		13	13		18	5	74	5	14	2	61
		6	2	72		27	12	50	75	15	10	1
	1		106	103		1	5	35				3
				15		4	31	10	27		5	11
			3	17			14	14	35			11
	5	3	23	9			10	106	37			29
	3	2	8	26	11	5	6	128	40		8	8
	3	2	12	37	5	19		22	26	14	2	20
Stems per H	41	16	277	498	35	95	90	479	281	133	27	152

Mountain material may illustrate the difference in populations to be expected in different environments, in this case on four directions of site exposure (Table 1).

A rather high degree of irregularity appears in these populations, occurring in an essentially Mediterranean climate with dry summers and consequent exposure to periodic fires of varying intensity. The differences in populations of the various species on different sites are, however, statistically significant.[*] The irregularity of these stands is only greater in degree than in some other areas; because of the instability inherent in the climax balance, because of the many chances of dispersal, occupation, etc., the figures can in any area be only average or most probable populations on a particular kind of site. We thus encounter in population problems of climaxes the probability effects in synecology indicated by Egler (1942).

In view of the irregularity and instability of climax populations it may well be asked whether the balance of populations is such that the distinction between climax and succession has meaning for population ecology. Since the climax condition may be defined by the steady-state, we may consider, first that the climax stand is less unstable than the seral stand and, second, that the seral stand differs in that its change is directional, fluctuating about no average. A third useful distinction is that succession usually has a definite starting point or time zero (Jenny 1941, Major 1951) in contrast to the continuing changes in the climax. So far as the steady-state distinction itself is concerned, it is likely that a steady-state of changing and developing character, incompletely stabilized with its balances gradually shifting, exists in many communities. Between the unstable early seral community and the fully stabilized climax may exist a wide area of intermediate conditions (cf. Alechin 1926). For the first distinction based on the steady-state criterion, it may be asked whether a slowly changing seral community, a Douglas-fir forest, say, is not more nearly stable than an herbaceous climax like the prairie. While satisfactory evidence is not at hand, it would seem that even a relative difference between seral and climax communities in extent of fluctuation may easily be broken down. For the second distinction it may be observed that short-term, irregular and rhythmic fluctuations are necessarily part of the seral community's functioning and that long-range, directional trends are necessarily imposed on climax communities by long-range physiographic and climatic changes. The distinction again breaks down, though meaningful as a relative difference. The distinction based on a definite starting point for seral changes must also

be qualified; for many of the changes occurring within the climax may have a definite starting point following a sudden climatic change, outbreak of an animal population, fire or wind effect, etc., while some successions, as the filling of a shallow lake and its replacement by forest, convert one type of self-maintaining community into another with no particular starting point for the change.

Evidence that the climax exists as a population phenomenon, as a community significantly less unstable than seral ones, is limited and largely circumstantial in nature. Such evidence includes (1) the observation that in some, climax stands the dominants are reproducing themselves while in other, seral stands they are not but are being replaced by the reproduction of other species; (2) the evidence that some, climax communities have not changed through a fairly long period of record while other, seral communities are more rapidly changing; (3) the observation that there is a fair degree of regularity in the appearance of similar population combinations on similar sites, suggesting that the populations have reached similar climax balances in their similar environments. It must be observed along with the last that some vegetations, as mature as they will become, e.g. the chaparral subject to burning and the unstable forests cited above, may not show any such regularity. It would seem that some communities may reach a climax in terms of growth-form, but never a steady-state of much meaning in terms of populations. While the climax may have surer significance in terms of growth-form, in terms of populations the climax, like the association, is a concept which tends to shrink under critical examination. It does not follow that it shrinks to nothing, and retention of the climax-succession distinction may still be justified.

INTERPRETATION OF EVIDENCE AND CRITICISM OF THE MONOCLIMAX

Before attempting further consideration of climax theory it may be well to compare the interpretations developed with the evidence already given. To be adequate, climax conceptions must provide for, or at least be consistent with, all lines of evidence available.

1. Succession. Evidence of successional characteristics—continuity and irregularity of populations, together with over-all trends—seem to agree well enough with the interpretation suggested. In this irregular continuum of populations our associes and myetia are, like our associations and ecotones, arbitrary and subjective, though justified by usefulness.

2. Climax convergence. If direction of succession and nature of the climax balance are determined in relation to environment, it should be expected that succession in similar environments would lead to climaxes having similar structural-functional patterns. Physiognomic convergence on a world-wide basis would be expected as similar community patterns developed to utilize resources in similar en-

[*] A test described by Mood (1950:398) indicates that the distribution of Castanopsis, *Quercus chrysolepsis*, and Arbutus, at least, differs significantly from random through the four series. The fact that the sclerophyll populations have more than one peak in the series of stations (e.g. Castanopsis with higher populations on mesic north and xeric south slopes than intermediate east and southeast ones) reflects actual bimodality of these populations, demonstrable with more entensive transect data, rather than sampling error.

vironments. Such convergence should be only partial, however, as observed by Beadle (1951), because of the different kinds of organisms available on different continents. Physiognomic convergence of vegetation of different sites in a single area might well occur in response to climate of the area, but should not be expected in all areas. Population convergence on similar sites in a limited area may also be expected, as a manifestation of community adaptation on the species level, at least in some areas.

3. Climax patterning. Because the sites occupied by communities are varied in any area, different climax populations are to be expected on them, adapted to site conditions. The climax vegetation of an area should consequently form a mosaic or pattern.

4. Climax continuity. Continuous change of site conditions along environmental gradients may be expected to imply continuous change in balance between growth-forms and species populations, little as we understand of the dynamics of such shifting balances. Granting the significance of vegetational discontinuities where they occur, the traditional conception of "a community" extending along a gradient essentially unchanged to some community-wide limit of tolerance where it is replaced by another community is, as a general principle, difficult to conceive dynamically if not meaningless semantically. It is suggested that vegetational change through space is as fundamental, as universal, and as generally continuous as vegetational change through time, even though discontinuities may be imposed on both spatial and temporal change.

5. Climax irregularity. Minor edaphic and climatic differences, chance factors of population entry, reproduction, and interaction, differences in history of past fires, insect attacks, windfalls, etc., may all contribute to the observed differences within a stand and from stand to stand on similar sites.

6. Climax instability. A degree of instability is intrinsic to the climax steady-state, and further instability results from effects of unstable environment on the balance.

As the evidence supports the conception of the climax as a population balance determined by the conditions of its site, some criticism of the monoclimax tradition in American ecology from Clements (1916) to Oosting (1948) and Braun (1950) may be indicated.

Analysis of monoclimax logic reveals that the position is not based upon a single conception, but upon two or more rather disparate ideas or assumptions. The monoclimax position, or any other climax position, must be brought into accord with the diversity of existing vegetation types in any area; and the harmonizing of existing diversity with theoretical unity of the monoclimax is by means of two assumptions. The first of these is the assumption of convergence to identity: "It is a fundamental part of Clements' concept that, given time and freedom, a climax vegetation of the same general type will be produced and stabilized irrespective of earlier site

differences." (Cain 1939:150). Since the convergence to identity quite evidently does not occur, a second assumption must be brought into play, the assumption of difference within identity. Different climax populations in an area are assumed to be different lociations or other sub-units of the same climax, and so the diversity of climax vegetation is provided for within the monoclimax (Cain 1939: 153).

It is the first assumption, of convergence to identity, which is the nucleus of the monoclimax theory. Vegetation is thought to develop, and as it develops to modify environment, to climaxes of equal mesophytism on different sites. From the extent of application and the extent of the covergences assumed, the belief seems to have been widespread in American ecology that nothing succeeds like succession. Because a degree of convergence among the seres in an area may be observed, and because in some areas all or most vegetation converges toward identity of dominant growth-form, if not of populations, in the climax, this assumption once seemed a reasonable one. But as a scientific theory judged for present validity, such an idea can scarcely stand against the great body of evidence of edaphic and other special climaxes. Because of the intimate relation of "environment," "vegetation," "soil," and "animal community" as aspects of the ecosystem, the conception of identical vegetation developing in different environments seems in fact an essentially implausible one. It is in opposition to the central ecological conception of organic systems adapted to their whole environments; this first monoclimax assumption seems to state that climax vegetation is both dependent upon environment (regional climate) and independent of environment (local and topographic factors) as if these two aspects of environment were separate in their action on living plants and in the functioning ecosystem. To the extent that the monoclimax theory is based upon the assumption of convergence to identity it may be rejected as both theoretically questionable and contrary to the bulk of existing evidence.

The second assumption of the monoclimax theory is that, since different self-maintaining populations occur on different sites in an area, these must be parts or subdivisions of the climax association. The characteristic terminological complexity of Clementsian ecology arose in part from this necessity of subdividing the climax. Along with the series of climax terms already indicated were the various -ations: the association, consociation, fasciation, and lociation, together with the seration and the more limited sociation, lamiation, and sation (Clements 1936). Further contributions have included the subassociation, the subsociation, (Woodbury 1933), association-segregate (Braun 1935a), presociation (Carpenter 1939), and biociation (Kendeigh 1948). In criticism of Clements himself it may be observed that his response to the problem of vegetation which does not come in simple, natural units was mainly through

multiplication of arbitrary units and sub-units. His answer to any new observation or exception, his way of meeting any new scientific challenge, was a new term. As a consequence the climax formation of Clementsian ecology might be described as a terminological jungle. Designation of the different types in a given vegetation pattern as preclimax, postclimax, etc., or as different consociations, lociations, association-segregates, etc., implicitly recognizes the non-convergence of climaxes. Justification of the monoclimax on the basis that north- and south-slope alternes, for example, are different lociations of the same association seems now to be a mere play with undefinable terms. To the extent that the monoclimax theory is based on the assumption of difference within identity it may be rejected as a semantic device which begs the question and obcures the problem.

When both these assumptions break down, as when climaxes which cannot belong to the same association exist in an area, a third provision is at hand—a set of words (pre-, post-, serelimax, etc.) to be applied to some of the climax types which do not fit into the climatic climax. These proclimaxes are often interpreted as arrested seral stages, potentially capable of developing to the climax (Clements 1928:106-7, 1936:262-4, Weaver & Clements 1929: 81, Phillips 1934-5:228). Since, however, they may be fully stabilized for their sites, they are subclimaxes which "only theoretically could be replaced by the climax" (Braun 1950:13). The recognition of a group of -climaxes which are neither actively developing nor true climaxes (Cain 1939:153), both stabilized and somehow developmental, is a position the logic of which does not commend itself. The necessity for these terms implying that some vegetation is climax, but seral also, may further illustrate the ambiguity and internal conflict resulting from imposition of the monoclimax ideal on actual vegetation.

Even apart from the proclimaxes, the monoclimax theory may be seen to be a mixture in indefinite proportions of two major propositions: that the various vegetation types in an area (1) are becoming the same climax or (2) are different parts of the same climax (Phillips 1934-5: 563, 566-7, Cain 1939:150, 153, Oosting 1948:223-4, 225-8, Braun 1950:12). These two assumptions are in a way complementary to one another. The second assumption provides for the failure of the full convergence assumed by the first to occur; the first permits the diversity of climaxes recognized by the second to be interpreted as dynamically related rather than as polyclimaxes. Perhaps it was the hybrid vigor from the union of these two ideas which permitted the monoclimax theory to persist so long in the face of so many criticisms by foreign ecologists and some by Americans. The two assumptions may seem somewhat in conflict since they state that the climaxes of two different sites are the same, but different. This conflict is not itself necessarily a major difficulty, since the as-

sumptions may be reconciled by considering that the convergence is only partial. If the convergence is only partial, however, climaxes of varying degrees of dissimilarity may be expected on different sites; and this is the basis of the polyclimax theory. Some sites, not too greatly different, will support climaxes which differ in populations but not in physiognomy; whether or not these are regarded as belonging to the same association is a matter of terminology and not of theory. Other differences in site will be expressed in differences of physiognomy; and the climaxes will, by convention, be assigned to different formations. In any area a number of climax types will occur and often these will include more than one physiognomic type or formation. Some modification of the polyclimax conception of a mosaic of climax types on different sites may result from the individualistic hypothesis and climax continuity, as indicated below.

The monoclimax theory is felt by the author to be clearly inadequate for the needs of analytical ecology. The view may be expressed that this theory is one of those uncritical, preliminary generalizations which are of the greatest value in stimulating research and furthering the growth of a field of science, but are later found untenable. Thus Clementsian "dynamic ecology" may be evaluated both as a valid and major contribution in its emphasis of process and as a system which was in part artificial and pseudodynamic, interpreting successional processes from situations where they are active to situations where they are not, and thus extrapolating these processes beyond their true effectiveness to the hypothetical monoclimax. It was the great contribution of Clements to have formulated a system, a philosophy of vegetation, which has been a dominating influence on American ecology as a framework for ecological thought and investigation and partly also as a basis for minority dissent. Some negative aspects of Clements' system may be recognized—the superficial verbalism, the tendency to fit evidence by one means or another into the philosophic structure, the thread of non-empiricism which runs through his thought and work—, but his service in providing and relating concepts, integrating ecological knowledge of his time into a conception of vegetation, may also be recognized. The Clementsian system had a certain symmetry about it, it was a fine design if its premises were granted; and for its erection Clements may rank as one of the truly creative minds of the field. Other ecologists of his time probably had clearer conceptions of some ecological problems, and further development of the field may stem less from Clements than from those who dissented from his system. The ecologist wrestling with ecological problems may often wish, however, that the field could be as neatly formulated today as it was by Clements, that the climax problem, for example, was as simple and non-relative as it seemed in Clementsian ecology—before the multiplication of terms was necessary because it was by no means so simple.

FORMULATIONS OF CLIMAX THEORY AND LOGIC

In place of the monoclimax, three major propositions on the nature and structure of climaxes and their relativity may be formulated:

1. The climax is a steady-state of community productivity, structure, and population, with the dynamic balance of its populations determined in relation to its site.

2. The balance among populations shifts with change in environment, so that climax vegetation is a pattern of populations corresponding to the pattern of environmental gradients, and more or less diverse according to diversity of environments and kinds of populations in the pattern.

3. Since whatever affects populations may affect climax composition, this is determined by, or in relation to, all "factors" of the mature ecosystem—properties of each of the species involved, climate, soil and other aspects of site, biotic interrelations, floristic and faunistic availability, chances of dispersal and interaction, etc. There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients and to other factors.

The following secondary or corollary propositions are suggested as of possible significance for synecological research:

A. Propositions of climax determination. Climax composition is determined, as indicated in (3) above, by all factors which are intrinsic to, or act upon, the population on a sustained or repeated basis and do not act with such severity as to destroy the climax population and set new succession in motion. Factors determining climax population will thus include:

1. Characteristics of the populations involved. The balance among populations will necessarily be determined by the kinds of populations entering the community and by the peculiarities of each. The place of a given species in the balance will depend on its ability to maintain a population against environmental resistance, determined by its genetics. Since genetics of species may change along gradients, changing genetics of the species should be part of the background of changing balance among species along gradients. Since a species differs genetically from one place to another, these genetic differences may influence the different places or degrees of importance of a species in climax balances.

2. Climate. All climaxes are adapted to climate (and hence are climatic climaxes); but the climate which acts on and determines a climax population is necessarily the local climate of its site, not the general climate of an area.

3. Site. The climax balance is determined by environment of a specific site, and the climax population has meaning only for a kind of site (Bourne 1934). For the early assumption that climax was independent of site may be substituted the hypothesis that any significant difference in site implies a difference in climax population. As all climax stands occur on sites having some kind of topographic relation to other sites, all climaxes are topographic, as well as climatic, climaxes.

4. Soil. Soil parent-material, as arbitrarily separated from other aspects of site, is a climax determinant; for the traditional assumption that vegetation on any soil parent-material converges to the regional climax may be substituted the hypothesis that any significant edaphic difference, physical or chemical, may imply difference in climax population. All climaxes are edaphic, as well as topographic and climatic, climaxes. The traditional distinctions among climatic climax, pre- and postclimax, physiographic or topographic and edaphic climaxes or paraclimaxes thus break down entirely, as indicated for climatic and edaphic climaxes by Lippmaa (1933b), Bourne (1934), Beard (1946), and Cain (1947). All are part of the climax pattern; all are adapted to climate and all other non-catastrophic factors of environment. The terms topographic and edaphic climaxes may have continued usefulness, however, to indicate that the topographic or edaphic distinctiveness of a site is to be emphasized in relation to the distinctiveness of a particular climax population in the vegetation pattern. The arbitrariness of any distinction between edaphic and topographic climaxes is well illustrated by Platt's (1951) recent work showing that "shale-barren" vegetation, as a recognized type, is determined by some sufficient combination of (1) properties of soil parent material, (2) steepness of inclination, and (3) dryness as affected by direction of exposure.

5. Biotic factors. Natural communities are organic systems of plants and animals in environment; in much of what has been said about the vegetation pattern might be substituted the more awkward phrase natural-community pattern. In the functioning system the balances among plant populations exist in relation to, and are partially determined by, animals acting directly on the plants through consumption and trampling, indirectly through soil, etc. All climaxes are biotic climaxes, balanced in relation to their animal populations. Designation of such cases as the grazing of bison in the Great Plains (Weaver & Clements 1929, Clements & Shelford 1939, Larson 1940), and of rabbits in Britain (Farrow 1916, 1917, Watt 1936, Fenton 1940, Hope-Simpson 1940) and the aspen parkland (Lewis et al 1928, Bird 1930), the vegetation of ant and termite colonies (Harshberger 1929b, Martyn 1931, Myers 1936, Burtt 1942, Fries & Fries 1948), prairie-dog towns (Scheffer 1937), and other animal societies, the effects of carp in a lake (Cahn 1929) and of guano deposits (Cockayne 1909, Summerhayes & Elton 1923, 1928, Steffen 1928, Polunin 1935, Russell & Wellington 1940, Rasmussen 1946, Grønlie 1948, Hutchinson 1950), the beaver-meadow complex (Ives 1942b), as biotic or disclimaxes implies no real distinction from other climaxes, but only that effects of animals are rather more evident to us than in other communities.

6. Fire. Periodic burning is an environmental factor to which some climaxes are necessarily adapted (Cooper 1922b, Show & Kotok 1924, Troup 1926, Petrie *et al* 1929, Wells & Shunk 1931, Chapman 1932, Grabherr 1936, Myers 1936, Humbert 1937, 1938, Robyns 1938, Aubréville 1938, Beadle 1940, Trochain 1940, Wells 1942, Rawtischer 1948, Weaver 1951a, Egler 1952). In areas where the fires affecting these climaxes are not set by lightning, they may be lit by native populations; in this as in other influences man, and especially aboriginal man, may be part of the ecosystem in relation to the various factors of which climax vegetation is determined. In the absence of fire the climax populations might well develop to something different; but such an ideal climax is not on the ground subject to measurement. The burning may cause some population fluctuation, and it may then be difficult to draw a distinction between fire (and windfall, etc.) as environmental factors to which some climaxes are adapted and as disturbances introducing still greater instability and initiating successions in others. A continuous series from climaxes fully adapted to fire and scarcely affected by a single burn, through climaxes in which minor changes are produced by each burning and those in which the vegetational structure is altered, but not destroyed, to climaxes which are entirely destroyed by a single fire may be expected. Without attempting to draw a clear line where none exists, it may be thought that, in fire-adapted climaxes, fire either does not destroy the dominant populations or does not cause replacement of the dominant growth-form as in other climaxes.

7. Wind. Although wind is a part of the environment of all climax stands, some stands may show marked effect of wind on composition or physiognomy, especially, toward higher latitudes and altitudes (Crampton 1911, Fries 1913, Braun-Blanquet 1913, 1932, Cockayne 1921, Scharfetter 1921, Szafer *et al* 1924, Brockman-Jerosch 1925-9, Allan 1926b, Cox 1933, Polunin 1934, Russell & Wellington 1940, Issler 1944), and other stands may have windfall permitting reproduction as a normal part of their relation to environment. The combination of sea-wind and salt-spray is particularly effective in producing locally distinctive climaxes along coasts (Crampton 1911, Boodle 1920, Nordhagen 1923, Pavillard 1928, Praeger 1934, Tansley 1939, Davis 1936, Bayer 1938, Wells & Shunk 1938a, 1938b, Wells 1939, 1942, Doutt 1941, Oosting & Billings 1942, Vesey-Fitzgerald 1942, Oosting 1945, Beard 1944b, 1946, Zohary 1947).

8. Other factors. Various other factors may determine locally what self-maintaining or climax populations can exist in a site including, for terrestrial communities, snow-effects (Heer 1835, Vestergren 1902, Smith 1912, Fries 1913, Braun-Blanquet 1913, 1932, Szafer 1924, Watson 1925, Nordhagen 1928, 1936, Lippmaa 1929, 1933b, Harshberger 1929a, Hansen 1930, Trapnell 1933, Cox 1933, Domin 1933, Böcher 1933, Hayashi 1935, Polunin 1935, 1936, Russell & Wellington 1940, Sørensen 1943, Lüdi

1948, Gjaerevoll 1950), fog as it affects the coastal redwoods (Cooper 1917), the fog vegetation of the Peruvian desert (Knuchel 1947), and the mossy or cloud forests of many tropic mountains (Shreve 1914a, 1914b, MacCaughey 1917, 1920, Brown 1919, Seifriz 1923, Holttum 1924, Lane-Poole 1925, Tate 1932, Richards 1936, Beard 1942, 1944b, Pittier & Williams 1945, Beebe & Crane 1947), salt water and tide levels affecting such coastal vegetation as mangrove swamps (Ainslie 1926, Chipp 1927, Marshall 1934, Stehlé 1945, Beard 1946, Dulau & Stehlé 1950, Egler 1952) and salt marshes (Johnson & York 1915, McCrea 1926, Conard 1935, Tansley 1939, 1941, Fontes 1945) although these, not simply seral communities which disappear to be replaced by a climax, may be incompletely stabilized (Vaughan 1910, Yapp *et al* 1917, Walton 1922, Nienburg & Kolumbe 1931, Steiner 1934, Richards 1934, Taylor 1938, Chapman 1938-41, 1940, Nordhagen 1940, Davis 1940, 1942, Purer 1942, Allan 1950, Navalkar 1951) migratory vegetation in the sense of Crampton (1911, 1912, Tansley 1929), communities of shifting equilibrium in the sense of Alechin (1926, 1927).

9. Floristics and faunistics. Climax composition will necessarily be determined by the plant and animal species available in the area. Climax populations in similar environments will vary from place to place for floristic and faunistic reasons, and a recognized climax population type or association will usually have a limited range (Lippmaa 1933b, Bourne 1934, Cain 1947).

10. Chance. Climax composition must, finally, be considerably affected by chances of dispersal and occupation (Palmgren 1929, Lippmaa 1935b) and of population interactions.

B. Propositions on climax relativity. It has been indicated that the climax population has meaning only relative to the environmental conditions of its site, and the inappropriateness of dichotomous logic has been indicated in several connections. The following aspects of climax relativism are suggested:

1. Climax and succession. There are no distinctions between climax and succession or, more concretely, between climax and seral stands, except those of relative instability and relative significance of directional change. This relativity was expressed by Cowles (1901:81), "As a matter of fact we have a variable approaching a variable rather than a constant," and has been indicated by various authors since (Cooper 1913, 1926, Braun-Blanquet & Jenny 1926, Gleason 1927, Braun-Blanquet 1932:322, Tansley 1939:228, Tutin 1941, Graham 1941).

2. Climax and seral species. There is no reason why some species should not be both seral and climax. Climax species may dominate succession as in desert successions (Muller 1940, Shreve 1942, 1951); a species may enter a stand in succession and persist at a different population level into the climax; a species may enter climax stands on one kind of site in an area but only seral stands on another (e.g. the Lake States pines, Eggler 1938, Grant 1934, Nichols 1935), and may enter climax stands in one area but only

seral stands in another (e.g. Douglas-fir, Munger 1940, Sprague & Hansen 1946, Hansen 1947, Merkle 1951). While some species seem clearly seral or climax under specific conditions, for many it is a question of relative position along the time-scale of succession under particular circumstances.

3. Climax and seral types. Types, associations, or stratal communities defined by species may, correspondingly, be seral in one circumstance and climax in another (e.g. pine and Douglas-fir stands, steppe in New Zealand, Zotov 1938, *cf.* Domin 1928a:26), or may be self-maintaining and successional at different times (Tansley 1939:234). Untenable is a familiar kind of logic: Type A (e.g. pines) is being replaced by type B (oak-hickory) on site number 1 (a north slope); therefore, type A growing on site number 2 (a southwest slope) will also ultimately be replaced by type B. Chain-linking of successional observations without regard for site (Type A was seen replacing type B, B replacing C, C replacing D, etc.; therefore, B, C, etc. are all seral to A) is also untenable (Gleason 1927).

C. Propositions on climax recognition. A number of criteria have been used either explicitly or implicitly in the traditional recognition of monoclimaxes (*vide* Cooper 1913:11, 1922b:75, Weaver & Clements 1938:479-80, Oosting 1948:229, Braun 1950:13). It may be profitable to examine some of these which seem no longer tenable in this section and to discuss some which seem applicable in the next section.

1. Unity of growth-form. "The first criterion is that all the climax dominants must belong to the same major life form, since this indicates a similar response to climate and hence, a long association with each other." (Weaver & Clements 1938; *vide* the revealing attempt to exclude *Tsuga canadensis* from the eastern forests for having the wrong growth-form, Clements 1934:64, 1936:258, Weaver & Clements 1938:83). The world-wide occurrence of communities of mixed dominance and of several physiognomic types within a given climatic area may be sufficient commentary.

2. Area of climax. The monoclimax has been thought to be climax of a definite geographic region, so that the climax could be recognized by essential similarity over a large area (Braun 1950) and occurrence of one or more of the dominants throughout the area (Weaver & Clements 1938). Areal extent is irrelevant to achievement of the climax steady-state, however; and there is almost no lower limit on the area of a climax type (Tutin 1941). Such restricted types as the summit balds of mountains (Cain 1930, Camp 1931, 1936, Brown 1941, Daubenmire & Slipp 1943, Merkle 1951), Appalachian shale barrens (Allard 1946, Platt 1951), and southeastern granite flat-rocks (McVaugh 1943), pines on altered andesite in Nevada (Billings 1950), stands as limited as the small marsh in a morainic depression and patch of "alpine rain-forest" at the head of a glacial valley described by Ives (1942a) are, if self-maintaining, climax vegetation. Removal of size restrictions on climax types has, with the variety of populations

present, the consequence that distinguishable climax types of the United States are essentially innumerable. While this must certainly be the case, stand types can very well be grouped subjectively into associations-abstract (Nichols 1917, Braun 1950) for some purposes.

3. Convergence on different sites. Convergence of different successions (Cooper 1913, Braun 1950) to similarity of vegetation on different sites (Cooper 1913, 1922b) is a criterion based on the first monoclimax assumption. The convergence is only partial, however, leading to climax vegetation which may be expected to differ on different types of sites. Granting the significance of such partial convergence on differing sites as occurs, it is not a basis of recognizing the self-maintaining condition.

4. Upland position (Nichols 1923). While the vegetation type prevailing on the uplands of an area may be more extensive than other types in the area, it is no more climax than they. Points 2, 3, and 4, may have meaning in relation to the prevailing climax, rather than in recognition of the climax steady-state.

5. Physiography. Convergence was achieved through both biological and physiographic processes in the interpretation of Cowles, but physiographic processes act through too long a period to be directly related to the climax as a biological phenomenon (Domin 1923, Faegri 1937). The consequence of erosion of an area down to a peneplain would be not to produce a uniform environment uniformly occupied by one of the vegetation types already in the area, but to produce a less diverse surface of different climate occupied by other kinds of climax stands. In spite of the impossibility of clearly separating biotic and physiographic (Cowles 1911), autogenic and allogenic (Tansley 1929, 1935) succession, it is the former, biological process, and not the hypothetical result of the latter, physical process, which is the concern of synecology (Michelmore 1934). Since some stands, at least, may reach the climax state in almost any area whether physiographically young, mature, or old, occupation of topographically mature sites (Braun 1950) may bear little relation to climax recognition.

6. Soil maturity (Braun 1950). While relations among climate, vegetation, and soil are recognized, these apply more to vegetation as growth-form than to vegetation as populations. As aspects of the ecosystem, vegetation and soil are, together, related to environment and one another, with neither simply determining the other (Jenny 1941, Major 1951). Soil, vegetation, and environment may consequently be expected to vary together, *pari passu,* through time and space; which is to say that the ecosystemic pattern varies in time and space and hence the coupled aspects of the ecosystem selected for study vary in parallel, though in no simple manner. The alternative definitions of soil maturity, in terms of profile development or of equilibrium with environment, are partially independent (Jenny 1941:48); and profile maturity of soil is not in itself a criterion of the climax state (Tansley 1935). Conditions of

some sites in any area and of most sites in some areas may be such as to prevent soils from developing to profile maturity as, in an extreme case, the "infantile" soils of the arctic (Griggs 1934). Soils in other areas may, in the course of development to the self-maintaining state, become degraded and podsolized so that a less productive vegetation and apparently less mature soil characterize the climax (Bourne 1934).

7. Mesophytism (Cowles 1901, Cooper 1913, Nichols 1917, 1923, Oosting 1948:224). The most mesophytic type of an area is no more "the climax" than other, less mesophytic, self-maintaining stands. The climax-adaptation index of Curtis & MacIntosh (1951) measuring relative mesophytism, etc., of stands is, as indicated by the authors, not simply a measurement of successional status. The course of succession will usually, though not necessarily, lead from apparently less mesophytic to apparently more mesophytic types; but it does not follow that a given xerophytic or hydrophytic stand is becoming more nearly mesophytic. A more mesophytic species is not to be chosen over a less mesophytic one as climax except as it is shown, for a given type of site, that the former replaces the latter. A balance between more and less mesophytic species may exist on sites too dry to support a purely mesophytic stand without implying succession.

8. Tolerance (Graham 1941). Succession will often involve more tolerant species replacing less tolerant ones, but in an area the more tolerant species may be climax on one site and the less tolerant ones on another. There is no reason why such intolerant species as the pines should not form climaxes, either in open stands in which they may reproduce continuously or in denser stands in which they may reproduce only periodically. There is no reason why more and less tolerant species should not form mixed climax stands, provided the stand is open enough to permit the latter to reproduce, or is sufficiently opened at times by fires, windfalls, etc., to permit the less tolerant species to reproduce. In general, in interpreting mixed stands, occurrence together of more and less mesophytic species, or of more and less tolerant species, or of species regarded from other evidence as climax and seral, may or may not mean that succession is occurring in the stand.

9. Higher growth-form (Weaver & Clements 1938: 90, 478). Apart from the difficulty of using criteria of higher and lower growth-forms (Gleason 1927) vegetational stature, at least, will usually increase through the succession into the climax. There is no reason, however, why heath, bog, or grassland should not in some areas replace forest as climax (Graebner 1901, Cajander 1913, Moss 1913, Backman 1920, Lüdi 1920, 1921, 1923, 1929, Katz 1926, Hopkinson 1927, Konovalov 1928, Zinserling 1929, Kleist 1929, Cain 1930, Mikyška 1932, Bayer 1933, Pfaffenberg & Hassenkamp 1934, Braun-Blanquet 1935, Ceballos 1935, Hausrath 1942, Duchaufour 1946-7, 1949, Killian & Moussu 1948, Zach 1950) even though such replacement violates our usual assumptions of trends

through succession and of forests as climaxes wherever forests occur. There is no reason why such simple and open communities as those of cliffs (Klika 1932, Davis 1951), hammadas (Cannon 1913, Zohary 1944, 1945), alpine rocks and scree (Hess 1910, Lüdi 1921, Frey 1922, Allan 1926a, Leach 1930, Jenny-Lips 1930, Lippmaa 1933b), and arctic fjaeldmark (Holttum 1922, Polunin 1934, Wager 1938) should not form self-maintaining stands or why the simple algae of a mountain lake should not form a "primitive" climax (Pennak 1951).

10. Relation to successional trends. As indicated for stature and soil, so for productivity, diversity, etc. These features of communities will usually increase through the succession to the climax, but there is no reason why, in a given case, the usual direction should not be reversed. In general, climax status should be determined not by abstract or generalized conceptions of what should be ultimate, but by what populations actually replace other populations and then maintain themselves.

APPLICATION

If the above criteria are to be limited or abandoned, we may seek what criteria of the climax state remain. Although the successional trends have been ruled out for climax recognition apart from site, they, and characteristics of self-maintaining populations, may be the basis of climax decision allowing for site differences.

1. Trends. If, on a number of similar sites, one finds sparse grass among rocks on some, Arctostaphylos heath with thin soil on others, and young red fir forests on a third group, it is reasonable to fit them into series from the first to the third on the basis of increasing community productivity and stature and soil maturity. If in addition the fir stands can be shown to be self-maintaining, it is reasonable to consider them the climax ending the succession. The trends may serve, with limitations in each case already observed, to relate types to one another in relation to succession and the probable climax.

2. Reproduction. In a self-maintaining forest population a J-curve of many young and few old trees (Meyer & Stevenson 1943) will often be encountered, so that there is agreement or accordance (Braun 1950:13) between canopy and reproduction. A climax forest stand may thus often be identified by its J-curve of age or size distribution, a seral stand by marked disparity between the canopy and an undergrowth of species able to grow to canopy stature on the site. Such J-curves, however, may be encountered in some seral stands and are not to be expected in unstable climax stands. While it has been indicated that pre- and postclimaxes, edaphic climaxes, etc., do not represent different kinds of climaxes, climaxes may be distinguished by types of reproduction and constancy or variation in dominance. Stands may reproduce continuously, cyclically, or irregularly, as indicated by Jones (1945) types of structure in virgin forests; and any of these modes of reproduction may occur in stands in which

the dominant species remain the same, while in other kinds of stands the dominant species may alternate cyclically (Watt 1947) or fluctuate and replace one another irregularly (Aubréville 1938).

3. Regularity within the stand. Climax stands often show a marked uniformity on sites of uniform conditions, seral stands are often, in contrast, patchy or irregular. Increasing uniformity in distribution of species in the stand through succession to the climax is the basis of Picchi-Sermolli's "maturity index" (1948a, 1948b), which has, however, as emphasized by the author, only relative, directive significance.

4. Regularity between stands. If the climax population is a balance adapted to environment, it may be expected that similar sites within an area will support similar populations; and such similarity of stands may be evidence of their having reached the climax state. The variation which is to be expected in climax stands may be measurable as a dispersion, indicating in part the degree to which vegetation is stabilized on these sites. When, on similar sites in an area, it is observed that one group of apparently undisturbed stands are very much alike and another group of diverse stands differ from these and one another, it may be reasonable to regard the former as climax and to fit the latter into succession by other criteria.

The phenomenon of stand-to-stand similarity on similar sites may thus be recognized as central to the climax problem. It is an important part of the evidence that the climax as a population steady-state exists, so that similar population balances will occur in similar environments. It is a principal means of recognizing the climax state where it occurs. In it also is the principal utility of the climax concept in research. The existence of stand-to-stand regularity makes possible study of climax populations and climax patterning, study which may exclude succession as an additional variable apart from climax problems as such. Treatment of all stands, seral and climax, together without regard to succession in many areas involves such a bewildering diversity of stands as to defy rational interpretation and relation to environment. Separation of climax and succession permits ordering of the data, in which those stands fully adapted to environment can be related to environment, and those becoming more fully adapted through succession can be related to environment and the time-scale of succession. Treating climax stands alone, their stand-to-stand regularity permits meaningful statements about average or most probable climax populations on a given type of site. Thus in permitting a statement, within probability limits, of what the climax population on a site of known environment but unknown vegetation should be, it meets a prime test of usefulness of a scientific concept or approach: possibility of prediction. It is suggested that a principal justification for retention of the climax concept is in this possibility. If regularity of stands is a principal justification for the

concept and for methods using the climax concept to study regularity of stands, a reciprocal interdependence of evidence, concept, and method exists, an interrelation which should be recognized, though it need not invalidate the approach through the climax.

Stand regularity may permit a further approach to climax definition. A climax stand is one which is self-maintaining and relatively permanent on its site (Tansley & Chipp 1926, Tutin 1941, Beard 1944a), but the individual stand is subject to fluctuation and shows chance variation from other stands. Of broader significance than the population of an individual climax stand is the average or most probable population for a type of site. Where data for several similar sites are available, the climax population may be defined as the average population of mature, self-maintaining stands on a type of site as defined and limited (see Table 1). Such an average population is not the absolute climax, which could not be determined if it existed, but is as close to the climax as we can come. Recognizing that there is no ultimate, absolute climax, we may substitute for the climax as an ideal the climax as a measured population; the climax population is the population of climax stands as measured. "The climax" may thus be defined by results of an operation, the counting (and averaging) of populations, though with subjectivity entering the choice of climax stands. In areas much disturbed, where climax stands cannot be measured, the climax may be without meaning as a population, while the alternative definition in terms of physiognomy may be sufficient for most purposes. In other areas largely undisturbed by man the climax populations may be so unstable and variable that averages have little meaning, and study of population changes within the climax communities may be more to the point (vide Graham 1941).

Available criteria of the climax state are far from providing for easy, objective identification of climax stands, nor can they be used securely without the judgment and feel for vegetational process of the research worker. In spite of attempts to increase the rigor of climax logic and method there remains an inescapable residuum of subjectivity. It may perhaps be recognized, in the character of the problem, why such must be the case. Not only is the difference between climax and succession relative, but all criteria applicable to the distinction are relative, partly independent of one another, and subject to a sufficient number of exceptions. In dealing with problems of climax and succession one may soon find oneself reasoning in such a network of relativities that some subjective choice of which of these are most significant is unavoidable. It is not surprising that Clements, facing this, sought to banish relativity from ecology, thus spiriting the fundamental difficulty out of sight. It was, however, one of the essential characteristics of the field which was thus apparently done away with.

Yet, in spite of the difficulties, effective methods can be applied in some areas for treatment of the

climax as a population.* A basis for some of these
may be found in the climax pattern conception. An
appropriate method of treating this pattern is that
of "gradient analysis" (Whittaker 1951, 1952), anal-
ysis of natural communities in terms of population
distributions along environmental gradients, an ap-
proach for which a theoretical basis is outlined by
Major (1951). As a population pattern climax vege-
tation should be suited to further statistical treat-
ment—averages and means of dispersion of climax
stands, correlation with environment and between
aspects of the ecosystem, etc.—than have yet been
undertaken.

One means of summarizing major features of the
pattern is its presentation in terms of the moisture
gradient, as in Fig. 1, or in terms of both moisture
and elevation (Whittaker 1951, 1952). In many areas
the vegetation of a given elevation on soil materials
not too diverse can be studied as a pattern of popu-
lations and types relative to the moisture gradient
(Linkola 1924, Alechin 1926, Arènes 1926-7, Mc-
Luckie & Petrie 1927, Phillips 1928, Sampson 1930b,
Hansen 1930, 1932, Pessin 1933, Grant 1934, Davis
& Richards 1934, Walter 1937, Pidgeon 1938, Hor-
ton 1941, Tolstead 1942, Wright & Wright 1948,
Morison *et al* 1948), to which vegetational pattern
a catena or pattern of soils (Milne 1935, Bushnell
1943, Morison *et al* 1948) may correspond. In many
areas several combinations of dominants may be
recognized along the gradient; but in northern and
mountain forests the canopy may be similar through-
out, while the gradient and other site differences find
expression in a diverse pattern of undergrowth types,
as recognized in the forest site types, etc., of Finnish
and other forest ecologists (Cajander 1909, 1926,
1943, Cajander & Ilvessalo 1921, Palmgren 1922,
Linkola 1924, 1929, Issler 1926, Klika 1927, Zlatník
1928, Juraszek 1928, Sukachev 1928, Ilvessalo 1929,
Kirstein 1929, Sambuk 1930, Borowicki 1932, Heim-
burger 1934, Meusel 1935, Lippmaa 1935b, Niedził-
kowski 1935, Müller 1936, 1938, Mikyška 1937, Arn-
borg 1940, Mallner 1944, Spilsbury & Smith 1947).
In either case, greater or less diversity of climax pat-
tern is to be expected, whether appearing in the
"associations" of dominants or only in the under-
growth.

A substitute for the climatic climax to charac-
terize a whole pattern may, finally, be sought in the
prevailing climax (Whittaker 1951). It may be de-
termined what dominant populations (or growth-
forms) are most numerous in the climax pattern, or
what type as defined (or climax physiognomy) oc-
cupies the majority of sites in an area. The pre-
vailing climax is thus quantitatively definable in terms
of either percentage of climax populations occurring
throughout an area or percentage of sites occupied
by an arbitrarily defined type. Through the prevail-
ing climax statements can be made about average
climax characteristics in an area, correlated with cli-
mate, with no assumption of convergence to a mono-

climax. In areas of complex environment and com-
plicated vegetation pattern, however, there may be no
prevailing climax type or growth-form; and average
stand composition for the area may have limited
meaning.

CONCLUSION

In the light of what has been said and what is,
in any case, familiar to practicing ecologists, the diffi-
culty, complexity, relativity, and subjective involve-
ments of climax theory and practice may be evident.
Vegetation presents a field of phenomena notably
lacking in fixed points of reference, lines of division,
invariable rules, and easy definitions. The spatial
pattern of natural communities is so complex that it
is beyond reasonable possibility to achieve under-
standing of it in full detail. Neither do we need to
seek such knowledge; two approaches on different
levels can be applied—extensive, geographic study
seeking generalized statements about major features
of the pattern, and intensive, analytical treatment
of local areas—to obtain different aspects of under-
standing desired. It is felt that the climax concept,
in terms of growth-forms or populations, may con-
tribute to both of these.

No completely rigorous definition of the climax
and its distinction from succession has been found,
and apparently none need be expected. If the re-
tention of the climax-succession distinction is to be
justified, presumably it must be not because the dis-
tinction is sharp and invariable, but because the dis-
tinction, relative as it is, has some real significance
and usefulness. While "climax" and "succession"
are only words referring to different degrees of in-
stability or of approach to a steady-state no longer
changing directionally, the distinction appears signifi-
cant; and in the absence of these terms it would be
necessary to refer to more or less stable, or more or
less mature stands, substituting other expressions.
In spite of all the difficulties the distinction has been
found useful in many research problems; in many
areas, at least, it has been found to work. Granting
the usefulness of the concept, the more clearly it can
be formulated the more serviceable a research tool it
may be. It has been an objective of this study to
show approaches toward less subjectivity and greater
rigor, to indicate research possibilities of quantita-
tive approaches to the climax free from some assump-
tions made in the past.

The interpretation developed, particularly that of
the climax as a population pattern, represents a
third climax hypothesis in addition to the traditional
monoclimax and polyclimax theories, a conception
which may be designated the climax pattern hypothe-
sis. This conception is in part intermediate to or
synthetic of the monoclimax and polyclimax, since the
diversity of climax stands is recognized, but these
are regarded, not as two or more discrete climax asso-
ciations, but as parts of a single, often continuously
grading climax pattern. Vegetation is conceived
as, even more fundamentally than the polyclimax
"mosaic of plant communities whose distribution is

* The following applications have been developed in more
detail in a manuscript, "A vegetation analysis of the Great
Smoky Mountains."

determined by a corresponding mosaic of habitats" recognized by Tansley (1939:216, cf. Domin 1929), a pattern of populations, variously related to one another, corresponding to the pattern of environmental gradients. Both the monoclimax and the polyclimax assume the existence of associations as valid, discrete units of vegetation, whether one or more than one of these may exist in a given area. The climax pattern hypothesis does not require the subjective grouping of both environments and stands into pieces of the mosaic; it is thus independent of the community-unit assumption and distinct from both the traditional theories. Evaluation of this concept against the monoclimax and polyclimax, as of these against one another, may be based on the criteria of simplicity of assumption, closeness of fit or correspondence to field observation, and methodological implication and productiveness.

The difference between the monoclimax and polyclimax has been recognized as semantic in part (Cain 1939, 1947) since ecologists may, in following one or the other, describe the same stands or stand types by different terms, or even by the same terms with different successional implications. The semantic aspect of the difference between these or among them and the climax pattern hypothesis by no means implies indifference of choice. Judged by simplicity of assumption, the polyclimax has the advantage over the monoclimax in freedom from the assumption of convergence in spite of difference in environment; and the climax pattern hypothesis may have the advantage over the polyclimax theory in freedom from the assumption that climaxes represent valid and distinct units or associations. Judged by correspondence to field data, the monoclimax is clearly least adequate, since the relation between the single ideal climax and the actual diversity of stands is abstract and arbitrary, and in fact somewhat remote. The polyclimax conception corresponds better to the diversity of stands, but implies that these belong to a definite number of distinct climaxes, while the climax pattern hypothesis allows in addition for the continuity of climax types and the diversity of stands only arbitrarily classifiable into a particular number of climax associations. The series—monoclimax, polyclimax, climax pattern—is thus regarded by the author as one of decreasing degree of abstraction and increasing closeness of fit to the actual pattern of vegetation, while the prevailing climax is a definable abstraction of higher order from the climax pattern to replace the undefinable climatic climax.

Judged in terms of methodological implication, the monoclimax is again least adequate, since it implies as a research approach the subjective choice of a climatic climax and the relation of other types in an area to this on a largely speculative basis. The polyclimax theory serves better for the study of actual successions observed to climax associations recognized; it permits both greater realism in the separation of concrete from supposititious successions and greater effectiveness in the relation of climax to environment, though retaining the community-unit assumption and the resulting mosaic conception. The climax pattern hypothesis, free from this assumption, permits the direct relation of community gradients to environmental gradients, of the whole diversity of climax stands in an area to the whole range of environments. The pattern conception and the emphasis of continuity lead to research methods relating populations of species and growth-forms to environmental gradients, to the approach of gradient analysis which is fundamentally different from the traditional approach through units. In methodological implication the climax pattern hypothesis differs more from the traditional two theories than these from each other; it is thus regarded by the author as both a synthesis of the other theories with open-system and population interpretations and an advance beyond them, a logical and natural development from the polyclimax. The difference among climax conceptions is, in any case, far from being a semantic quibble or straw-man tactic (Egler 1951); it is one of the most important decisions to be made by synecologists and one for which quite adequate bases of choice exist.

It is the author's hope that some convergence of the divergent schools of ecology might be possible on the basis of this and other approaches which in part synthesize, in part develop beyond differences among schools. It is surely to be regretted that plant ecology has so largely lacked, since the early great figures in the field, the world-wide perspective which is to be sought in all fields of science and is an achievement of many. Contact is not what it should be even between American and British ecologists (Godwin 1949), and the two major groups of Continental ecologists have been equally divided from one another (Faegri 1937). The alienation of American and Continental ecology in matters other than method is all too familiar. One basis of this may be in some of the interpretive inadequacies rather characteristic of traditional American plant ecology, recently pointed out by Egler (1951). The difficulty may also, however, lie in the difference in relative emphasis of succession and climax and relative size of the "fundamental units" used: the series—American, British, Swiss-French, and Scandinavian—is, on the whole, one of decreasing emphasis of succession and climax and decreasing magnitude of principal vegetational units. It may be observed that these two concepts which separate American and Continental ecology, the monoclimax and the association, are both subjective; and it would scarcely seem that these subjective concepts constitute grounds for divorce between ecological schools. An intermediate position can be conceived, one free from the overemphasis of climax and succession among many American ecologists and the underemphasis among many Europeans, free from the overemphasis of terminology and classification of units in both, and more concerned with dynamic process within the community and with vegetational problems on a world-wide scale. This best common denominator of American and Continental ecology is essentially the position occupied

for some time by British ecology. The viewpoint developed here differs from the British tradition in the full abandonment of the climatic climax (except in the definable form of the prevailing climax) and the conception of natural communities and environment as forming together an ecosystemic pattern subject to analysis. Perhaps in the development of analytical approaches to natural communities and of concepts more closely related to analysis and its results, the differences among schools in classificatory and descriptive concepts and abstract interpretation may lose their present importance.

SUMMARY

1. A brief review of the development of climax theory in different schools of ecology indicates the confusion existing and the need for reconsideration of the concept.

2. Some of the evidence bearing on the problem may be summarized as: 1) continuity and irregularity of populations in succession, and 2) convergence, 3) patterning, 4) continuity, 5) irregularity, and 6) instability of climaxes. Adequate conceptions of climax and succession must be consistent with these lines of evidence and sufficiently general in formulation to provide for climax phenomena on a worldwide and not a regional basis.

3. Common to succession and the climax is the interplay of populations, which in succession is expressed in directional change and in the climax as fluctuation about an average. In the progressive development from originally unorganized populations of an organized community pattern adapted to environment, succession is an evolutionary process in a general sense. Through the course of succession there tends to be progressive increase in community complexity and diversity, stature or massiveness and productivity, maturity of soil, and relative stability and regularity of populations; but exceptions to all these trends may be noted. Certain successions involving marked decrease in productivity and others of the above may be termed, by definition, retrogressive.

4. The climax may be interpreted as a partially stabilized community steady-state adapted to maximum sustained utilization of environmental resources in biological productivity. As a functioning system developing in relation to environment, the natural community has a structural-functional pattern adapted to the whole pattern of environmental factors in which it exists. Similar or convergent community patterns tend to develop in adaptation to similar environments. Change in environment implies change in the community pattern; and along a continuous environmental gradient, community composition will usually change continuously.

5. These interpretations appear consistent with the evidence. The climatic climax or monoclimax theory is regarded as untenable.

6. Three principal propositions of climax theory are offered:

1) The climax is a steady-state of community productivity, structure, and population, with the dynamic balance of its populations determined in relation to its site.

2) The balance among populations shifts with change in environment, so that climax vegetation is a pattern of populations corresponding to the pattern of environmental gradients, and more or less diverse according to diversity of environments and kinds of populations in the pattern.

3) Since whatever affects populations may affect climax composition, this is determined by, or in relation to, all "factors" of the mature ecosystem—properties of each of the species involved, climate, soil, and other aspects of site, biotic interrelations, floristic and faunistic availability, chances of dispersal and interaction, etc. There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients and to other factors.

Secondary propositions are developed from these. All climaxes are topographic or physiographic, edaphic, and biotic, as well as climatic; many are determined in relation to fire, wind-effects, snow, salt-spray, etc.; and all may be affected by "chance" factors. Distinctions between climax and succession, climax and seral species, and climax and seral types or stands are necessarily relative. Various of the traditional criteria of climax recognition (unity of dominant growth-form, area of climax, physiography, soil maturity, upland position, mesophytism, tolerance, higher growth-form) are wholly or partially irrelevant for the recognition of the climax state.

7. Useful aids to recognition of the climax state are: successional trends, with limitations and for particular sites, observed reproduction, regularity within stands, and stand-to-stand regularity. The last is central to climax theory as an evidence that a climax steady-state exists, as a means of recognizing the climax state, and as a basis of the principal utility of the climax in research. The climax may be defined by the average population of mature, self-maintaining stands on a type of site as defined and limited. Subjectivity is not eliminated from such a definition nor, from the nature of the problem, can it be. The climax may often be analyzed and represented as a pattern of populations along the moisture gradient, or in relation to this and other gradients. In some areas a prevailing climax may be defined, as a replacement of the climatic climax, by the percentages of dominant species in the pattern or by the percentage of sites occupied by a type as defined.

8. For all its subjectivity and relativity, the climax concept has real meaning and usefulness. The climax pattern hypothesis developed here represents a third climax conception, preferred over the traditional monoclimax and polyclimax theories, and a basis for the research approach of "gradient analysis." It is to be hoped that, with the recognition of the subjectivity of the association and climatic climax and increasing use of analytical approaches, some convergence among the divergent schools of ecology may be possible.

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